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A synopsis of the pre-human avifauna of the Mascarene Islands

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Abstract — The isolated Mascarene Islands of Mauritius, Réunion and Rodrigues are situated in the southwestern Indian Ocean. All are volcanic in origin and have never been connected to each other or any other land mass. Despite their comparatively close proximity to each other, each island differs topographically and the islands have generally distinct avifaunas. The Mascarenes remained pristine until recently, resulting in some documentation of their ecology being made before they rapidly suffered severe degradation by humans. The first major fossil discoveries were made in 1865 on Mauritius and on Rodrigues and in the late 20th century on Réunion. However, for both Mauritius and Rodrigues, the documented fossil record initially was biased toward larger, non-passerine bird species, especially the dodo *Raphus cucullatus* and solitaire *Pezophaps solitaria*. This paper provides a synopsis of the fossil Mascarene avifauna, which demonstrates that it was more diverse than previously realised. Therefore, as the islands have suffered severe anthropogenic changes and the fossil record is far from complete, any conclusions based on present avian biogeography must be viewed with caution.

Key words: Mauritius, Réunion, Rodrigues, ecological history, biogeography, extinction

Introduction

The Mascarene Islands of Mauritius, Réunion and Rodrigues are situated in the south-western Indian Ocean (Fig. 1). Despite their comparatively close proximity to each other, each island differs topographically and the islands have generally distinct avifaunas. The Mascarenes were the last major group of islands to be colonised by humans, so remained in a comparatively pristine state into the era of written history. Arab traders were aware of them from at least the 13th century and the Portuguese in the early 16th century (NORTH-COOMBES 1980, 1994a; HALL 1996), but as far as known no attempt at settlement was made by either. It was with the chance discovery by a Dutch East India Company (VOC) fleet under Vice-Admiral Wybrandt Warwijck in September 1598, who claimed Mauritius for the Netherlands, that the documented history of the Mascarenes began (MOREE 1998; CHEKE & HUME 2008). The endemic fauna was sketchily described or illustrated in ships' logs and journals, which became the source material for popular articles and books and, along with collected specimens, enabled monographs such as that by STRICKLAND & MELVILLE (1848) on the dodo Raphus cucullatus (LINNAEUS, 1766) to be produced. STRICKLAND and MELVILLE based their osteological analysis on the surviving remnants of a dodo once exhibited at the Ashmolean Museum in Oxford, and a dodo foot preserved in the British Museum in London (HUME et al. 2006). For the next two centuries, the islands' ecosystems were irreversibly destroyed due to anthropogenic activities, which resulted in the extinction of the majority of endemic vertebrates (CHEKE & HUME 2008). The discovery of subfossil material in 1786 on Rodrigues (although the first major discovery was not made until 1865), in 1865 on Mauritius and in the late 20th century on Réunion resulted in the description of new avian fossil taxa and also provided some corroboration with species described in early accounts. In gen- 196 -



FIGURE 1. Map of the Southwestern Indian Ocean showing the Mascarene Islands of Réunion, Mauritius and Rodrigues. From CHEKE & HUME (2008).

eral, only the larger and more distinct avifauna was described from the fossil record, whereas other avian orders, *e.g.*, smaller passerines, were ignored. As a result, determining avian biogeography based on current knowledge of fossil avifaunas is problematic.

This paper provides a synopsis of the prehuman Mascarene avifauna based on recent, more comprehensive studies, using a combination of palaeontological and historical evidence. It addresses the taxonomic problems associated with erroneous identifications and descriptions, and will hopefully provide an important resource for those interested in avian phylogenies and avian biogeography of the region. All taxa considered to be endemic or indigenous to the islands are covered, including extant species, those known from the palaeontological record, and those species known only from contemporary accounts that almost certainly once existed, but have not yet been discovered in the fossil record. But I must emphasise that work is not yet complete. A number of subfossil elements that almost certainly represent further new taxa have been discovered, but the lack of suitable diagnostic specimens and/or suitable comparative material has held back identification. The original Mascarene avifauna must surely have been even more diverse than the results presented here suggest.

Study area

Geology and Physiography: The isolated Mascarene Islands are volcanic in origin, and have never been connected to each other or any other landmass. Réunion (21.0° S, 55.5° E), the most southerly of the islands, lies 665 km east of Madagascar, whereas Mauritius (20.25° S, 57.5° E) is situated 164 km east north-east of Réunion. Rodrigues (19.75° S, 63.5° E) is the most remote, lying 574 km east of Mauritius and approximately 4800 km west of Australia.

Mauritius (Fig. 2) is approximately 60 km long by 40 km wide, with a surface area of 1865 km². As well as being smaller, it is also much lower than Réunion, with Black River Peak being the highest point at 828 m. The broad undulating lava plains of the north rise to a maximum of 152 m above sea level, intersected in the middle of the island by mountains, the rim remnants of a former caldera. Mauritius is surrounded by a reef-fringed lagoon, averaging 0.8 km wide, but on the east coast reaching 5 km, whereas on two short stretches of the west and south coasts, the sea breaks directly onto the cliffs (CHEKE & HUME 2008). There are a number of islets within the lagoon; the most biologically important being the northern islets, which are the only places where some endemic reptiles and seabird colonies have managed to survive.

Mauritius emerged around 10 Ma, and was built by three volcanic episodes (SADDUL 2002). After a shield-building phase and deposition of the Old Lava Series between 7.6 Ma to 5 Ma, subdued volcanic activity commenced with the formation of a caldera. A new phase of volcanism occurred between 3.5 and 1.7 Ma leading to the formation of the Early Lava Series. A third phase of active volcanism commenced at 0.7 Ma and lasted until 20 Ka, forming the Intermediate and Recent Lava Series (DUNCAN & HARGREAVES 1990; RUSDIJK *et al.* 2009).

Réunion (Fig. 3) is the largest and highest of

the Mascarene Islands, being 70 km long by 50 km wide and covering 2,512 km², with over 60% of the land surface being above 828 m (NICHOLLS 2006). It has the highest peak in the Indian Ocean, the Piton des Neiges, which rises to over 3,069 m. Its second highest peak at 2,631 m is the Piton de la Fournaise or Le Volcan, an active volcano that is situated to the east of a volcanic hotspot. It is probably the same hotspot that during the past 66 Ma gave rise to the enormous Deccan Traps lava fields in India, the Maldives, the Chagos, the Saya de Malha, Nazareth and St.Brandon (Cargados Carajos) banks (large undersea plateaus), and to Mauritius (CHEKE & HUME 2008). The centre of Réunion is divided into massive cirgues, each dissected by extremely deep gorges. Around the island, the land shelves steeply into deep water, sometimes under massive sea cliffs. There is virtually no fringing reef and, where coral has developed close inshore, only a narrow lagoon exists.

Réunion is the youngest of the Mascarene Islands and emerged from the surface of the sea approximately 2.8 Ma (McDougall et al. 1971). The island comprises two coalesced volcanoes, the Piton des Neiges, which forms two thirds of the island in the northwest, and the Piton de la Fournaise in the southeast (DUNCAN & HAR-GREAVES 1990). The construction or first phase of the Piton des Neiges includes two main events, the first dating back 2.1 to 0.43 Ma, and the second more explosive phase, which is divided into three events, occurred from 0.35 Ma to less than 30 Ka. The first and second began almost simultaneously around 230 Ka, with the third around 188 Ka. During this time, the Piton de la Fournaise, which began erupting approximately 360 Ka, collapsed several times into the ocean (see MOURER-CHAUVIRÉ et al. 1999 for a detailed summary). The combination of these events may have eliminated the original avifauna.

Rodrigues (Fig. 4) is the smallest of the Mascarene Islands, being 17.7 km long and by 8.45 km wide, with a surface area of 104 km². It has a central ridge with steep, incised valleys extending to the coast, and its highest point, Mont Limon, is just 398 m. The island is surrounded by a vast, submarine platform, of which an area of about twice that of the land surface is occupied by an extensive reef-fringed lagoon (CHEKE & HUME



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FIGURE 2. Map of Réunion Island showing the original vegetation, and the fossil localities mentioned in the text. From CHEKE & HUME (2008).

2008). The lagoon has a number of islets comprising mainly flat calcarenite limestone, though some have basaltic hills, sandbanks or small basalt outcrops. These islets provided refugia for elements of the original fauna decades after their populations had been extirpated on the Rodrigues mainland (HUME 2007, 2011). Rodrigues has been dated at 1.5Ma (McDOU-GALL *et al.* 1965), which would make it the youngest of the Mascarene Islands, but this is not supported by geomorphology and the degree of endemism (CHEKE & HUME 2008). More recent work suggests an age similar to that of Mauritius (GIORGI & BORCHELLINI 1998). Although Rod-



FIGURE 3. Map of Mauritius showing the original vegetation and the fossil localities mentioned in the text. From CHEKE & HUME (2008).

rigues is mainly composed of basaltic lavas, it has a large limestone plateau (calcarenite) on the southwest coast called the Plaine Corail, which was formed from the accumulation of windblown coral sand. MONTAGGIONI (1973) thought that formation occurred around 80 Ka during the last glacial, however, current consensus suggests that they form during interglacial periods, and not glacial, so date determination remains unknown. **Climate:** The Mascarenes lie within the southeasterly trade winds, but during the austral summer months (January, February, March) tropical cyclones and depressions associated with the seasonal movement of the ITCZ (Inter Tropical Convergence Zone) have a marked effect on the islands. Rainfall is seasonal, with a dry season from May through to October under the influence of the cool and dry easterly trade winds, with a wetter, warmer season from November

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FIGURE 4. Map of Rodrigues Island showing the fossil localities mentioned in the text. From CHEKE & HUME (2008).

to April, when the ITCZ is in its southernmost position (SENAPATHI et al. 2010). Depending on relief and slope orientation to prevailing winds, mean annual rainfall on Mauritius varies from 800 mm in the western coastal lowlands and 1400 mm in the eastern coastal lowlands to 4000 mm in the uplands (PROAG 1995). Mean annual temperature is 22°C (MAURITIUS METEOROLOGICAL SERVICES 2012). On Réunion, the central massifs create a rain shadow, which exposes the east of the island to prevailing easterly winds creating wet and cloudy conditions most days of the year (CHEKE & HUME 2008). Réunion is one of the wettest places on earth, averaging 6-7 m of rainfall per year on the wettest coast to 10-12 m inland (SOLER 2000). The coastal leeward area in the west is very dry with average rainfall of 540 mm per year. Mean annual temperature is 23°C on the coast, but the temperatures drop progressively inland and upslope. Rodrigues is the driest of the islands, with rainfall averaging from 800 mm on the Plaine Corail in the coastal southwest to > 1,600 mm in the central-west uplands (CHEKE & HUME 2008). Mean summer temperature is 25.9 °C and mean winter temperature is 22.3 °C (MAURITIUS METEOROLOGICAL SERVICES 2012).

History of palaeontological research

The first fossil material discovered on Mauritius was found in a marshy deposit known as the Mare aux Songes in the southeast of the island in 1865. Harry HIGGINSON, a railway engineer who was working on the Midlands stretch of the Mauritius railway, noticed that labourers were

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stock-piling bones while digging peat from the marsh. The embankment of the Midlands stretch ran close to the northern edge of the Mare aux Songes. HIGGINSON informed George CLARK, a diocesan teacher in Mahebourg, who had been searching for 20 years for fossil remains on Mauritius (CLARK 1866; HUME et al. 2009). CLARK had a copy of the aforementioned dodo monograph by STRICKLAND & MELVILLE (1848), and from the illustrations he was able to identify dodo remains (HUME et al. 2009). CLARK obtained permission to work the site, and sent consignments of dodo material to Richard OWEN, Superintendent of Natural History Departments at the British Museum, who formally described the dodo's anatomy (OWEN 1866a). Due to CLARK's monopolisation of the Mare aux Songes and his overriding interest in selling dodo bones for monetary gain, almost no other vertebrate species were collected (HUME et al. 2009). Owen received a parrot mandible in one of the dodo consignments, and this was the only fossil bird species described during this time (OWEN 1866b; HUME et al. 2009).

A second more thorough excavation of the Mare aux Songes was organized under the guidance of Théodor SAUZIER in 1879, from which six new fossil bird species were described (NEWTON & GADOW 1893), but few contextual details were obtained. In the early years of the 20th century, Paul CARIÉ, whose family owned the estate containing the Mare aux Songes, sent more bird material to Paris (HUME 2005), and further very minor excavations took place up to the 1930s; however, no more new bird species were described. The Mare aux Songes was infilled with dolomite gravels and boulders in the 1940s, in an effort to prevent the spread of malaria (HUME *et al.* 2009), after which the site was all but forgotten.

In 2005, the fossil deposit was reinvestigated by a Dutch team researching human-induced changes to the environment. In June the following year, an interdisciplinary team including geologists, geophysicists, palaeobotanists, palaeontologists, and geneticists began a major excavation, which has continued annually until 2011 (RIJSDIJK *et al.* 2009; RIJSDIJK *et al.* 2011). The Mare aux Songes contains an integrated vertebrate Konzentrat-Lagerstätten, with a high diversity of macrofossils, including seeds, branches, leaves, insects, snails and even fungi, and microfossils (pollen, diatoms, ostracods), buried in a matrix of organic material.

Elsewhere on Mauritius, Etienne THIRIOUX, an amateur naturalist, excavated cave and boulder-field deposits around Le Pouce Mountain, and lava caves at Pailles, Roches Noires and the Vallée des Prêtres in the late 1890s and early 1900s (HUME 2005), but the exact locations were not specified (but see below). Thirioux collected thousands of bird skeletal specimens including an almost complete, associated Mauritius Red Rail Aphanapteryx bonasia (Sélys-Longchamps, 1848) and a dodo. Other cave deposits were discovered in 2007, 2008 and 2009 by myself and colleagues at Plaine des Roches, Vieux Grand Port and La Prairie (JANOO 2005; HUME 2007, 2011), including another associated but badly degraded dodo at Bois Cheri, in the central highlands (MIDDLETON & HUME in press).

No fossil history existed for Réunion Island prior to 1974, when Bertrand KERVAZO excavated cave deposits at Grotte des Premiers Française about 1.5 km southwest from St. Paul, from which three new fossil species were described (KERVAZO 1979; COWLES 1994). During the 1980s, four other fossil localities were discovered, the Grotte de l'Autel; Grotte "au Sable" (sic) and Caverne de la Tortue cave sites, and the coastal swamp, the Marais de l'Ermitage, all on the northwestern side of Réunion (MOURER-CHAUVIRÉ & MOUTOU 1987; MOURER-CHAUVIRÉ *et al.* 1999).

Although the first Rodrigues subfossil solitaire Pezophaps solitaria (GMELIN, 1788) material had been collected in 1786 from caves on the Plaine Corail, the specimens were not described until 1848 (Strickland & Melville 1848). GMELIN (1788) had based his description on the solitaire account of BUFFON (1766), and not from any physical evidence. Major excavations of the caves began in the late 1860s and early 1870s (GÜNTHER & NEWTON 1879; HUME et al. 2009). Cowles (1987) visited the Plaine Corail as part of the British Ornithologists' Union expedition in 1974, and mentioned, but did not describe, two potentially new fossil species. I searched all previously excavated caves and collected numerous subfossil remains from undisturbed caves over a 10 year period commencing in 2000, from which one new species has been described (HUME 2011) and at least three more await description.



FIGURE 5a. The Mare aux Songes photographed by the author in 2007.

The fossil deposits

Mauritius

Mare aux Songes - The Mare aux Songes is situated in southeast Mauritius, approximately 0.5 km from the coast (Figs 2, 5a), and was created by the collapse of a large lava tube system. It comprises four sub-basins separated by rock thresholds, and sub-basins I, II and III are bordered by <15 m rock cliffs. Sub-basins 0, I and II contain (or contained) subfossil material; all recent excavations took place in sub-basin I. The basaltic base rock of sub-basin I is situated 8–10 m below sea level, and is overlain by ~ 8 m thick sedimentary succession. The succession is divided into five distinct sedimentary units. The bedrock is overlaid by $\sim 1 \text{ m}$ of grey clay with very low concentrations of organic material (Unit A), covered by ~ 6 m of fine to medium carbonate sands with some infiltration of organic matter (Unit B). Above this lies a ~100 mm thick calcareous gyttja (Unit C), which is overlaid by a ~ 500 mm thick fossiliferous layer (Unit D). The matrix of Unit D is made up of woody material, nuts and seeds, all interspersed with amorphous peat, and contain 99% of all fossil material (Fig. 5b). This layer is capped by introduced dolomite boulders and gravel (Unit E) (RIJSDIJK et al. 2009). Sub-basin 0 is now destroyed and sub-basin II is completely infilled with Unit E. Sub-basin III has the same sedimentological units as sub-basin I, but these vary in thickness. Comparatively few subfossil remains are present, however. 14C dat-



FIGURE 5b. Detail of the Mare aux Songes fossil layer, Unit D. A tarsometatarsus of a dodo *Raphus cucullatus* (centre) is surrounded by the remains of giant tortoises *Cylindraspis* sp. The matrix is made up of seeds, leaves and other plant debris. Photograph courtesy of Ranjith JAYASENA (Amsterdam).

ing and sedimentological analysis has shown that 4000 Ka the marsh was a fresh water lake that acted as an oasis in an otherwise dry environment (RIJSDIJK *et al.* 2009; RIJSDIJK *et al.* 2011; MEIJER *et al.* 2012).

Le Pouce Mountain — The exact localities where THIRIOUX was collecting on Le Pouce Mountain (Fig.2) cannot now be determined. A survey by the author, Owen GRIFFITHS and Greg MIDDLETON in 2007 discovered a previously excavated large rock overhang in boulder scree at 350 m in Le Pouce valley, beneath Snail Rock (HUME 2011). As no one else is known to have worked in this area, this overhang might be one of THIRI-OUX's original collecting sites.

Plaine des Roches — Subfossil remains of dodo have been found in the extensive lava tube systems at Plaine des Roches (JANOO 2005). In general, the cave sediments are thin or non-existent, the majority of which are covered with collapsed cave debris. The material is poorly preserved, but appears to represent a natural accumulation. There are numerous large or small openings (pit-fall traps) in the roofs of the caves (Fig. 6), into which the native fauna fell and was unable to get out.

Vallée des Prêtres — A number of THIRIOUX fossil specimens were supposedly collected in the Vallée des Prêtres, but it is uncertain if this was the true area of provenance. Some specimens have Vallée des Prêtres locality data written on the museum labels, yet they were collected from the Mare aux Songes (pers. obs). The Vallée des Prêtres is situated on the west flank of Le Pouce Mountain, above and to the north of the capital, Port Louis (Fig. 2). It is steep-sided and arid, and sparsely covered with introduced trees and shrubs. I have not located any caves or large boulder overhangs in the valley, but there is a substantial amount of boulder scree. It is possible that Thirioux collected fossil material from sediment deposits amongst the rocks.

Kanaka Cave, Bois Cheri — The discovery of a complete, but badly degraded dodo (Dodo Fred) (Fig. 7) in Kanaka cave, Bois Cheri, in the highlands of Mauritius (Fig. 2) resulted in much media interest (MIDDLETON & HUME In press). The basaltic cave was infilled with roof collapse debris and was extremely humid. Sediments included massive clay bedding interspersed with <5 mm rock fragments, and fine clays and silts. The dodo specimen was partially exposed on bare rock, with the bulk of the skeleton collapsed into a small crevice. This confirmed that dodos once occurred in the highlands as well as the lowlands.

Vieux Grand Port — Near the site of the Dutch fort at Vieux Grand Port (Fig. 2) is a small limestone outcrop, which has a number of small caves. The Dutch used some of these caves for shelter, as purpose-built animal corrals have been constructed inside. The caves are dry, and fining upwards silts reach a depth of up to 300 mm in the deeper recesses. Well preserved subfossil remains have been found buried at depths of 100 mm, including the type specimen of *Nesoenas cicur* HUME, 2011.

La Prairie — La Prairie is a limestone plain on the southwest coast (Fig. 2), which contains a number of caves. Some are permanently filled with water. The sediments comprise silts intermixed with roof collapse debris and can reach depths of 500 mm. The caves contain the remains of native birds and reptiles, and the deposits are particularly rich in *Pteropus* fruit bat remains.

Baie du Cap — JANOO (2005) and his colleagues discovered probable human-predated dodo remains in cliff caves at Baie du Cap (Fig. 2), on the south-west side of Mauritius. A single phalange supposedly exhibits knife marks, but the specimen needs analysis under SEM (Scanning Electron Microscope) to confirm this.

A number of additional fossil localities have been discovered on Mauritius containing the remains of giant tortoises *Cylindraspis* sp. (Aus-



FIGURE 6. Palaeontologist, Lorna STEEL, beneath a roof opening in Twilight Caverne, Plaine des Roches, Mauritius.

TIN & ARNOLD 2001; BOUR 1984; FLORENS 2002), but bird remains are rare or absent in these. They include cave and boulder overhangs at Ile aux Aigrettes, Les Quatre Cocos, Flacq, 'Mt. Zaco'(west of Brise Fer Mountain), Palma, Camp de Masque, Trois Mamelles and Corps de Garde Mountain. Marsh deposits include Mare du Puit; La Mare La Chaux; Mare Sèche; and Riche Mare. Subfossil tortoise remains were also found in sand dunes at Flic en Flac (FLORENS 2002), but the area has now been completely developed.

Réunion

This is a summary only; for a complete review see KERVAZO (1979); COWLES (1994); MOURER-CHAU-VIRÉ & MOUTOU (1987); & MOURER-CHAUVIRÉ *et al.* (1999).

Marais de l'Ermitage — The Marais de l'Ermitage is the only swamp/marsh fossil deposit on Réunion (Figs 3 and 8). The surface sediments comprise an 800 mm thick organic soil (peat?) layer, which is virtually fossil-free. This overlies a 300–400 mm fossil-rich horizon



FIGURE 7. The associated, but badly degraded remains of dodo *Raphus cucullatus* (Dodo Fred) in Kanaka cave, Bois Cheri. Photograph courtesy of Greg MIDDLETON (Hobart).



FIGURE 8. Avian palaeontologist, Cécile MOURER-CHAUVIRÉ (centre) (UCBL), Sonia RIBES (left) (MHN-RUN), Roger BOUR (right) (MNHN), and co-workers excavating the Marais de l'Ermitage, Réunion. Photo courtesy of Roger BOUR (MNHN).

intermixed with basaltic rocks and coral, resting on marine sediment made up of coralline sands, coral fragments and marine molluscs (MOURER-CHAUVIRÉ *et al.* 1999). The fossil layer is dominated by giant tortoise *Cylindraspis indica* (SCHNEIDER, 1783), with comparatively rare bird and bat remains. The depositional setting of the Marais de l'Ermitage is somewhat similar to that of the Mare aux Songes on Mauritius. Unfortunately, a substantial part of the swamp has now been developed, and the remaining area is also at risk of destruction.

Caverne de la Tortue — This is in the only lava tube system on Réunion, and is situated around 250 m above sea level (Fig. 3). Entrance to the cave is via a roof opening, which drops 5 m to the cave floor. Most subfossil remains were found around the entrance, and were extremely fragile. They included the type, probably associated individual of Réunion rail, *Dryolimnas augusti* MOURER-CHAUVIRÉ *et al.* (1999).

Grotte des Premiers Française (Grand Caverne) — This large cave was first excavated by KERVAZO (1979), and subsequently by MOURER-CHAUVIRÉ et al. (1999) (Fig. 3). It is a prehuman deposit and dominated by two species of shearwater Puffinus sp. Discoveries include the type of Alopochen kervazoi (COWLES, 1994), and a left distal femur fragment of Fregilupus varius (BOD-DAERT, 1783), the only known subfossil passerine bone so far discovered on Réunion.

Grotte de l'Autel — This small cave (Fig. 3)

was completely excavated in 1980 and contained a number of subfossils, including a humerus of the Réunion pink pigeon, *Nesoenas duboisi* ROTHS-CHILD, 1907a, one of only two known, and numerous remains of the Réunion ibis, *Threskiornis solitarius* (SÉLYS-LONGCHAMPS, 1848).

Grotte "au Sable" — This is another small cave (Fig. 3), in which subfossil remains are dominated by *Puffinus* shearwaters (MOURER-CHAUVIRÉ *et al.* 1999). The deposits included some introduced species, so was contemporary with the first settlers on the island.

Caverne à Cotte — JOUANIN & GILL (1967) examined a cave system at 1800 m in elevation, overlooking the Rivière des Remparts, and discovered a smaller chamber about 10 m from the main cave. They discovered cranial and post cranial remains of *Pterodroma baraui* in the sediments. No other details are given.

Rodrigues

There are large numbers of caves and small fissures on the Plaine Corail (Figs 4 and 9), many of which contained subfossil remains. Here I describe only those cave localities that have contributed significantly to our knowledge of the pre-human Mascarene avifauna.

Canyon Tiyel — Canyon Tiyel was probably created by roof collapse of an extensive cave system on the Plaine Corail (Fig. 10). The canyon has a 30 + m high rock face at the northwest end,



FIGURE 9. Cave expert, Greg MIDDLETON (Hobart), entering an unexplored cave on the Plaine Corail. Note the dense covering of introduced, invasive *Lantana* scrub, which now makes locating new caves extremely difficult.

which tapers off to approximately 10 m at the southern end, and a number of caves are situated at the base or on top of the canyon walls. The basal sediments are at least 10 m in depth and have been accumulating since the Pleistocene (BURNEY *et al.* in prep.). The sediments are poor in pollen and subfossil remains.

Caverne Poule Rouge — This cave has proved to be the most palaeontologically productive in recent years (Fig. 11). The cave sediments range from 850 mm in the centre of the cave to <10 mm at the extremities, with the majority of specimens found on or in the uppermost sediments. I discovered a complete, associated male solitaire in 2005, partially buried in flow stone (Fig.12). Other skeletal material retrieved from the site includes the type of *Alectroenas payandeei* HUME, 2011, and remarkably preserved tortoise scutes (outer horny covering), which still retain the original blackish colouration.



FIGURE 10. Canyon Tiyel looking south. Caves are located at the base of the canyon walls and along the top ridges of the canyon.

Caverne Gastonia — Caverne Gastonia (Fig. 13) is a pit-fall cave with a unique, small pool at the furthest point from the entrance. The pool water is so lime (CaCO₃) saturated that precipitated lime flakes form on the water surface, before gently sinking and settling into three underwater mounds. Subfossil remains are partially buried in flowstone throughout the caves, but most loose specimens were found on the surface or buried up to a depth of <200 mm beneath the entrance.

Caverne Tortue — This cave has deep sediment deposits which have slumped away from the entrance, which contained disarticulated elements of many native birds. The rest of the cave has sediments averaging <100 mm in depth, except in a few deep recesses.

Caverne l'Affouche — Caverne l'Affouche has proved extremely productive. It is a deep, wide cave with heavy roof collapse forming a steep scree slope within. Rich fossil deposits



FIGURE 11. Lorna STEEL (NHMUK) entering a chamber in Caverne Poule Rouge.



FIGURE 12. A complete, associated solitaire *Pezophaps solitaria*, partly buried in flow stone in Caverne Poule Rouge. Photograph courtesy of Lorna STEEL (NHMUK).

occur between boulders and overhangs. Finds include an associated solitaire, a probable new passerine, and numerous disarticulated specimens of native birds.

Caverne Dora — Caverne Dora is situated at the southern end of Canyon Tiyel, and contains a series of narrow corridors and small caves. Excavation at the entrance (Fig. 14) unearthed remains of various birds, including owls, herons (Fig. 15) and hundreds of endemic reptile elements. The site entrance may have been utilised by the Rodrigues lizard owl *Mascarenotus murivorus* MILNE-EDWARDS, 1874. One of the owl elements found in this deposit was used for 14C dating (see below).

Caverne Solitaire — Caverne Solitaire is the only cave I have studied that has a distinct sedimentological unit, compared with the general uniform sediment deposits seen in other Rodrigues caves. Beneath a rock overhang lies a \sim 300 mm thick unit made up of coarse, angular >50 mm cave debris in a matrix of reddish silt/clay. Embedded in the matrix are pieces of wood and individual bird elements, including shearwater *Puffinus* sp. This unit probably represents a flash flood during a severe cyclonic event, when surface debris and bird bones were washed into the cave.

Caverne Bambara — Three large and connecting caves make up the Bambara series. The largest (Bambara I) is open at both ends and it has been used as a shelter for farm stock. Bambara II and Bambara III are more interesting as the cave floors have not been trampled. Sediments reach a depth of 300 mm in places, and excavations of the caves have resulted in the collection of a large number of subfossil remains, including a partially associated Rodrigues turtle dove *Nesoenas rodericana* (MILNE-EDWARDS, 1874) (HUME 2011).

Grand Caverne — This is the largest cave in the Plaine Corail area, and has been used extensively for livestock housing; thus the cave floor is heavily trampled. A large pit is still present in the centre of the cave, which may have been one of the 1874 Transit of Venus excavation sites. Despite the effects of long-term domestic animal occupation, a number of subfossil bird remains have been found in small side chambers, and in undisturbed sediments at the edges of the cave walls.

Anse Mourouk — Mourouk is a coastal dune site, situated in south-central Rodrigues. A complete femur of *Pezophaps solitaria* was recovered during the excavation of a whale skeleton by the author and colleagues in 2007. This is the first subfossil bird bone found on Rodrigues outside of the Plaine Corail.

Age of the fossil deposits

14C dating of dodo, tortoise *Cylindraspis* sp, wood and seeds from the Mare aux Songes on Mauritius suggest an extremely narrow time window for fossil accumulation, with a calibrated age range of ca 4235 to 4100 cal. yr BP (averaged 14C age of 4200 yr BP for date of deposition) (RIJSDIJK *et al.* 2011). This contrasts with two



FIGURE 13. Entering Caverne Gastonia through the roof opening. Most of the subfossil remains were found directly beneath the entrance. Photograph courtesy of Lorna STEEL (NHMUK).

museum specimens of *Cylindraspis* sp. obtained by GÜNTHER *c*. 1870, which yielded significantly younger radiocarbon ages, between ca 1260 and 1830 BP (BURLEIGH & ARNOLD 1986).

On Réunion, radiocarbon dates obtained for bones of *Cylindraspis indica* (SCHNEIDER, 1783) from the Marais de L'Ermitage give dates ranging 915 ± 120 BP (interval in real years after calibration 883–1273 AD) and 1755±40 BP (interval in real years after calibration 186–391 AD), and those of introduced *Sus scrofa* LINNAEUS, 1758 associated with *C. indica* 365±35 BP (interval in real years after calibration 1458–1633 AD) (MOURER-CHAUVIRÉ *et al.* 1999).

Two 14C dates have been obtained from Rodrigues. One taken at 10 m from basal sediments in Canyon Tiyel gave a date of 8490 ± 40 BP (interval in real years after calibration 9540– 9460 BP) (BURNEY *et al.* in prep.). Another 14C date taken from a partial humerus of the extinct Rodrigues lizard-owl *Mascarenotus murivorus* (MILNE-EDWARDS, 1874), excavated from sediment at a depth of 65–75 mm in Caverne Dora, dated to 2850 ± 30 BP (interval in real years after calibration 3060-2870 BP (BURNEY *et al.* in prep.). The latter dating is indicative of extremely slow sediment depositional rates within the caves themselves.

Palaeovegetation

While we have a comparatively good idea of



FIGURE 14. Excavation of Caverne Dora showing Square A. Note the almost uniform and featureless sediments, common to most cave deposits on the Plaine Corail.

the original macrofauna on the Mascarenes, the composition of the palaeo-vegetation is more difficult to determine. This is particularly true in the most devastated parts of the islands, *i.e.*, in the coastal and lowland areas, which were probably the prime habitat of many of the endemic vertebrates including the dodo. As these habitats were drier and more open, they were more accessible to humans and vulnerable to fire; hence they were the first areas to be destroyed. Mauritius and Réunion have a wetter windward side on the east side, with a drier zone on the leeward side in the west. Early accounts report that on all three islands, dense canopy forests occurred down to the coast on the windward side, with perhaps a more open, palm-rich forest on the lee (CHEKE & HUME 2008). Réunion is a high island with much of its vegetation above 800 m, comprising montane wet forest, heath and upland bogs. As a result, it has the best surviving habitat. Rodrigues was completely forested according to LEGUAT (1708), being especially dense in the lowland valleys, whereas Pingré (NAGEPEN 2004) recorded that the forest was thick but stunted on the Plaine Corail: most of the island is now deforested

Recent excavations at the Mare aux Songes have proved invaluable in determining the original composition of lowland forest on Mauritius (RIJSDIJK *et al.* 2009). The marsh is situated in a lowland coastal area on the windward side of Mauritius, but receives an average rainfall below 1200 mm, the same average as on the dry, coastal leeward side (LONGMAN 2007).



FIGURE 15. A sternum of the Rodrigues night heron *Nycticorax megalocephalus* on surface sediments in Caverne Dora.

The Mare aux Songes contained forest components from marsh, dry and wet forest zones. The most common species in the deposit is the wet forest tree, tambalacoque Sideroxylon grandiflorum (Sapotaceae), which is endangered and confined to mountain forests today. Other wet forest genera include Canarium (Burseraceae), Eugenia (Myrtaceae), Elaeocarpus (Elaeocarpaceae), Diospyrus (Ebenaceae) and the endemic palm genus Dictyosperma (Arecaceae). Dry forest genera comprise Foetidia (Lecythidaceae), lowland species of Sideroxylon (Sapotaceae), Stadmania (Sapindaceae) and two species of the palm genus Latania (Arecaceae), one now extinct (FLORENS pers. comm.). Cassine (Celastraceae) occurs in both wet and dry forest zones. At least four species of screw pines Pandanus (Pandanaceae) have also been identified from the deposit, including dry, wet and upland marsh species, indicating that they were once an important component of the lowland coastal forests.

Species accounts (see Tables 1 and 2)

Taxonomic nomenclature follows Howard and MOORE (DICKINSON 2003).

Ducks and Geese (Anatidae)

Ducks and geese were mentioned on numerous occasions in early accounts, but almost all provide few descriptive details.

Anas theodori — The Mascarene teal once occurred on Mauritius and Réunion, and was last recorded around 1700 on Mauritius and in 1710 on Réunion (HUME & WALTERS 2012). Osteological studies of postcranial bones have shown that the two populations were undifferentiated, so the birds were almost certainly capable of flying between the islands (MOURER-CHAUVIRÉ *et al.* 1999; CHEKE & HUME 2008). The Mascarene teal was described from postcranial bones collected from the Mare aux Songes (NEWTON & GADOW 1893), and more recently from postcranial material collected in the Marais de l'Ermitage swamp on Réunion, and are most similar to the Austral teal *Anas gibberifrons* (MÜLLER, 1842) (MOURER-CHAUVIRÉ *et al.* 1999). COWLES (1994) referred a fragmentary cranium from the Mare aux Songes to *A. theodori*, which differs from that of any other *Anas*.

Alopochen mauritianus — The Mauritian sheldgoose was mentioned in 1681 as 'inhabiting the woods and dry ponds' (CHEKE 1987; YOUNG et al. 1997), which suggests that it was probably becoming terrestrial. They were last reported in c. 1700, so presumably died out shortly after. The Mauritian sheldgoose was described from a partial pelvis and complete carpometacarpus excavated from the Mare aux Songes. Recently, a tarsometatarsus, the first known, was collected there in 2006 (RIJSDIJK et al. 2009). Furthermore, I have identified a radius, which was erroneously referred to Nycticorax mauritianus by Newton & GADOW (1893), as also belonging to Alopochen. Mascarene geese are derived from the Egyptian goose Alopochen aegyptiacus (LINNAEUS, 1766), and the available elements of A. mauritianus are smaller than A. aegyptiacus.

Alopochen kervazoi — The Réunion sheldgoose was discovered in a number of cave deposits and also in Marais de l'Ermitage swamp. It had disappeared by the end of the 17th century due to over-hunting. *A. kervazoi* differs from *A. aegyptiacus* in having a more robust tarsus and a short, deep bill (CowLES 1994; MOURER-CHAUVIRÉ *et al.* 1999).

Aythya sp. — BERNARDIN (1687) and BOUCHER (1710) both mention 'sarcelles et canards' in Réunion, thereby identifying two species from their observations. MOURER-CHAUVIRÉ *et al.* (1999) found two carpometacarpi of an *Aythya* sp. in the Marais de l'Ermitage, a genus present on Madagascar, Southeast Asia and Australia, as well as *Anas theodori*. The Madagascar pochard *Aythya innotata* SALVADORI, 1894 is most similar



FIGURE 16. A reconstruction of the Mare aux Songes, Mauritius around 4 Kya. Every species depicted here, including the flora, has been found as a fossil in the marsh deposits. Of the vertebrates, only the echo parakeet *Psittacula echo*, pink pigeon *Nesoenas mayeri* and Mauritius kestrel *Falco punctatus* survive today. Illustration by the author.

to the Réunion *Aythya* species, so it may well have been this species or something closely related to it that once occurred on Réunion. Nothing more is known about it.

Stout-legged duck — A single femur discovered in 2009 in Caverne Poule Rouge, Rodrigues, is referable to a small duck, approximately the size of *Anas bernieri* (HARTLAUB, 1860). No endemic anatids are known from Rodrigues, but an account by BOUWER (reprinted in MOREE 2001), sailing with the fleet under Wolfert HARMENSZOON in 1601, stated that he landed on Rodrigues and collected some wild geese (HUME 2003). The bone is robust with a and comparatively lateromedially compressed at the proximal end. More material is needed before any further diagnoses can be made.

Petrels and Shearwaters (Procellariidae)

It is difficult to ascertain the former diversity and abundance of petrels on the Mascarenes. Early accounts report large breeding colonies of various species, particularly on the islets around Mauritius and Rodrigues, but there must have been a number of local extinctions. Furthermore, some very distinct but enigmatic species are known from just a few sightings and even fewer specimens.

Pseudobulweria atterima — The Mascarene Black Petrel is critically endangered, rarely seen and its breeding areas, thought to be confined to Reunion, have only recently been discovered (TATAYAH *et al.* 2011). A single specimen has been collected on Mauritius (*ibid*). BOURNE (1968) described and figured subfossil remains of a petrel from Rodrigues cave deposits, ascribing them



FIGURE 17. A reconstruction of Canyon Tiyel, Rodrigues around 1 Kya. Every species depicted here has been found as a fossil in the cave deposits. Of the vertebrates, only the two small passerines, the Rodrigues fody *Foudia flavicans* and Rodrigues warbler *Acrocephalus rodericana*, and Rodrigues fruit bat *Pteropus rodricensis* survive today. Illustration by the author.

to *Pseudobulweria atterima*. This was in error as my re-examination of the material shows that the elements are too large and they differ in other characters. CowLes (1987: p. 93) mentioned, but did not describe, the same material, referring it to *Pterodroma*. On Rodrigues in 2008, I found numerous cranial and post-cranial petrel remains, which represent a new, but now almost certainly extinct taxon. It is larger than any petrel known in the region.

Pterodroma arminjoniana — An unidentified species of *Pterodroma*, which bred on Round Island off the north coast of Mauritius, was only recently identified as Trinidae Petrel (BROWN & JORDAN 2009). It may have only colonised the island since the early 1900s (VINSON 1976). Numerous recent skeletal remains can be found on Round Island, but the species is unknown in the fossil record.

Pterodroma baraui — Barau's petrel is an elusive, endangered species that breeds at high

elevations on Réunion (PINET *et al.* 2009). CHEKE (1987) noted that he found a small breeding colony of Barau's petrel on Rodrigues in 1974, but subsequent searches failed to find them. Subfossil remains have been collected from Caverne à Cotte, a cave situated at 1800 m in elevation on Réunion (JOUANIN & GILL 1967).

Puffinus iherminieri — Two widespread *Puffinus* shearwaters once bred on Mauritius and Réunion. Audubon's shearwater is no longer resident on Mauritius, but still breeds on Réunion. Subfossil remains of this shearwater are common in Réunion cave deposits, including numerous juvenile specimens (MOURER-CHAU-VIRÉ *et al.* 1999).

Puffinus pacificus — The wedge-tailed shearwater breeds only on a single islet off Réunion, but it is abundant in cave deposits on the mainland. It is still common on Mauritius (STAUB 1976), and I discovered skeletal remains in boulder scree below Le Pouce Mountain, and an associated individual in a cave at La Prairie. On Rodrigues, it bred on Ile aux Fregate (STAUB 1973, 1976), but my survey of this islet in 2005 failed to locate any birds; feral cats were abundant, and may have exterminated the population. Subfossil remains of this petrel are rare on Rodrigues, but specimens were collected in 1874, all held at the NHMUK, from unspecified caves on the Plaine Corail.

Grebes (Podicipedidae)

No species of grebe is known to have inhabited the Mascarenes. The supposed extinct species *Podiceps gadowi* HACHISUKA, 1953 is based on a mis-identified bone of a whimbrel *Numenius phaeopus* LINNAEUS, 1758 (CowLes 1987; see wader accounts below).

Flamingos (Phoenicopteridae)

Phoenicopterus ruber — During the early years of human occupation, greater flamingos were a resident breeding species on Mauritius and Réunion, with stragglers occasionally reaching Rodrigues (CARIÉ 1930; CHEKE 1987). Flamingos originally numbered in their thousands and were still considered common during the mid 18th century, but were systematically hunted for food. They were extirpated, or had dispersed from Mauritius by *c*. 1770 and from Réunion by *c*. 1730 (CHEKE & HUME 2008). Subfossil remains have been recovered from the Mare aux Songes, Mauritius (NEWTON & GADOW 1893), and Marais de l'Ermitage, Réunion (MOURER-CHAUVIRÉ *et al.* 1999), including juvenile specimens.

An enigmatic and hypothetical species, the *Géant*, has created a wealth of literary debate, which is really not deserved. The existence of *Géant* is based entirely on the account of LEGUAT (1708), who described a bird the height of a man, with a goose-sized body, long neck and legs, and goose-like but pointed bill. He observed a number of them on Mauritius, but saw it only once on Rodrigues. The *Géant* was subsequently described as a valid taxon, *Leguatia gigantia* SCHLEGEL, 1866, and placed in Rallidae, a proposal ardently supported by ROTHSCHILD (1907a), HACHISUKA (1953) and NORTH-COOMBES (1983). However, LEGUAT also mentions a rose-coloured underwing, which

is an important diagnostic character. No rail is known to have any red under the wing (OLSON 1977), but flamingos certainly do. With no evidence to the contrary, it seems almost certain that LEGUAT had observed a flamingo.

Ibises (Threskiornithidae)

Threskiornis solitaries — Ibis of the genus Threskiornis occur only on Madagascar and Aldabra in the Indian Ocean, and another species occurred historically on Réunion (MOURER-CHAU-VIRÉ & MOUTOU 1987; MOURER-CHAUVIRÉ et al. 1995a, b, 1999). It was called the solitaire by the local inhabitants. The solitaire declined once humans settled on the island, gradually retreating into the remote mountain tops as the island became more populated (CHEKE 1987; HUME & WALTERS 2012). The last account to refer to them was in 1708, so they must have died out shortly afterwards (HUME & WALTERS 2012). Subfossil remains have been found in the Marais de l'Ermitage, Grotte des Premiers Française and Grotte de l'Autel (MOURER-CHAUVIRÉ et al. 1999). It was a derivative of either the sacred ibis T. aethiopicus (LATHAM, 1790), which occurs on Madagascar and Aldabra, or possibly strawnecked ibis T. spinicollis (JAMESON, 1835) from Australia, Indonesia and New Guinea (ibid).

More speculation and misinterpretation has been made about a white dodo on Réunion than any other Mascarene bird, save the dodo of Mauritius (HUME & CHEKE 2004). Reports were made during the 17th and early 18th century of a large white bird that could be caught easily and lived alone in the mountains (MOURER-CHAUVIRÉ et al. 1999). These descriptions, which are certainly referable to the solitaire (MOURER-CHAUVIRÉ et al. 1999), were subsequently associated with some white dodo paintings by two Dutch artists, Pieter HOLSTEYN II and Pieter WITHOOS (NEWTON 1869), which elevated the Réunion white dodo Raphus solitarius Sélys-Longchamps, 1848 into the realms of scientific credibility (HUME & CHEKE 2004). However, no dodo fossil remains have been found on Réunion, whereas the discovery of subfossil remains of an ibis confirmed the solitaire's threskiornithid relationships (MOURER-CHAUVIRÉ et al. 1999), a bird that better corresponds with the descriptions in early accounts.

Common name	Original Latin name & authority	Current Latin name	Mauritius	Réunion	Rodrigues
Mauritius sheldgoose	Sarkidiornis mauritianus Newton & Gadow, 1893	Alopochen mauritianus	†FE	_	_
Réunion sheldgoose	Mascarenachen kervazoi Cowles, 1994	Alopochen kervazoi	-	†FE	_
Mascarene teal	Anas theodori Newton & Gadow, 1893	Anas theodori	†FE	†FE	_
Réunion pochard	<i>Aythya</i> sp. (see Mourer- Chauviré et al. 1999)	Aythya sp.	_	†FE	_
Barau's petrel	<i>Pterodroma baraui</i> Jouanin, 1964	Pterodroma baraui	_	Е	†Ε
Trinidade petrel	<i>Aestrelata arminjoniana</i> Gigioli & Salvadori, 1869	Pterodroma arminjo- niana	Ind	_	_
Mascarene black petrel	<i>Procellaria atterima</i> Bona- parte, 1857	Pseudobulweria at- terima	EV	Е	?
Audubon's shearwater	<i>Puffinus iherminieri</i> Lesson, 1839	Puffinus iherminieri	FInd	FInd	_
Wedge-tailed shear- water	<i>Puffinus pacificus</i> Gmelin, 1789	Puffinus pacificus	FInd	Find	FInd
Greater flamingo	<i>Phoenicopterus ruber</i> Lin- NAEUS, 1758	Phoenicopterus ruber	†FInd	†FInd	†V
Réunion ibis or soli- taire	<i>Apterornis solitarius</i> Sélys- Longchamps, 1848	Threskiornis solitarius	-	†FE	-
Mauritius night heron	Butorides mauritianus New- TON & GADOW, 1893	Nycticorax mauritianus	†FE	_	-
Réunion night heron	<i>Ardea duboisi</i> Rothschild, 1907a	Nycticorax duboisi	-	†FE	_
Rodrigues night heron	<i>Ardea megalocephalus</i> Milne-Edwards, 1874	Nycticorax megalo- cephalus	_	_	†FE
Green-backed heron	<i>Butorides striatus</i> Linnaeus, 1758	Butorides striatus ssp.	†?F		†?F
Javan green-backed heron	<i>Butorides striatus javanicus</i> Horsfield, 1821	Butorides striatus javanicus	Ind	Ind	Ind
Dimorphic egret	<i>Egretta dimorpha</i> Hartert, 1914	Egretta dimorpha	†FInd	†Ind	-
Red-tailed tropic bird	Phaethon rubricauda Bod- DAERT, 1783	Phaethon rubricauda	Ind	Ind	Ind
White-tailed tropic bird	<i>Phaethon lepturus</i> DAUDIN, 1802	Phaethon lepturus	Ind	Ind	FInd
Greater frigate-bird	Fregata minor GMELIN, 1789	Fregata minor	IndV	IndV	IndV
Lesser frigate-bird	Fregata ariel GRAY, 1845	Fregata ariel	IndV	IndV	IndV
Red-footed booby	Sula sula Linnaeus, 1766	Sula sula	Ind	-	Ind
Masked booby	Sula dactylatra Lesson, 1831	Sula dactylatra	Ind	Ind	-
Abbott's booby	Sula abbotti Ridgway, 1893	Papasula abbottii	†Ε	-	†Ε
Mauritius darter	* <i>Plotus nanus</i> Newton & Gadow, 1893	Phalacrocorax (Micro- carbo) africanus	-	_	_
Reed cormorant	<i>Phalacrocorax africanus</i> Gmelin, 1789	Phalacrocorax (Micro- carbo) africanus	†FE?	†E?	_

TABLE 1. Systematic list of Mascarene bird species mentioned in the text including extant species, recently extinct species known from museum skins, and those known from subfossil remains only. Key: * = Misidentified; $\dagger =$ extinct; E = endemic; Ind = indigenous; V = vagrant; F = fossil; S = museum skin.

TABLE 1.	(continued).
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Common name	Original Latin name & authority	Current Latin name	Mauritius	Réunion	Rodrigues
Mauritius kestrel	Falco punctatus TEMMINCK, 1821	Falco punctatus	FE	_	_
Réunion kestrel	Falco duboisi Cowles, 1994	Falco duboisi	_	†FE	_
Réunion harrier	<i>Circus maillardi</i> Verreaux, 1862	Circus maillardi	†FΕ	Е	-
Réunion rail	<i>Dryolimnas augusti</i> Mourer- Chauviré, Bour, Ribes & Moutou, 1999	Dryolimnas augusti	_	†FE	_
Mauritius or Sauzier's wood rail		Dryolimnas sp.	†FE	_	_
Mauritius red rail	<i>Apterornis bonasia</i> Sélys- Longchamps, 1848	Aphanapteryx bonasia	†FE	_	_
Rodrigues rail	<i>Erythromachus leguati</i> Milne-Edwards 1874	Erythromachus leguati	-	_	†FE
Common moorhen	<i>Gallinula chloropus</i> Lin- NAEUS, 1758	Gallinula chloropus	Ind	Ind	_
Mascarene Coot	<i>Fulica newtoni</i> MILNE-Ed- wards, 1867b	Fulica newtoni	†FE	†FE	-
Madagascar button- quail	<i>Tetrao nigricollis</i> Gmelin, 1789	Turnix nigricollis	-	Ind?	-
Whimbrel	<i>Numenius phaeopus</i> Lin- NAEUS, 1758	Numenius phaeopus	FInd	FInd	Ind
Mauritius grebe	* <i>Podiceps gadowi</i> Hachisu- ка, 1953	Numenius phaeopus	-	_	-
Curlew	<i>Numenius arquata</i> LINNAEUS, 1758	Numenius arquata	Ind	Ind	Ind
Dodo	Didus ineptus LINNAEUS, 1766	Raphus cucullatus	†FSE	_	_
Rodrigues solitaire	Didus solitarius Gmelin, 1788	Pezophaps solitaria	_	_	†FE
Mauritian wood pigeon	<i>Columba thiriouxi</i> Hume, 2011	Columba thiriouxi	†FΕ	_	-
Mauritius pink pigeon	<i>Columba mayeri</i> Prévost & Knip, 1843	Nesoenas mayeri	FE	_	_
Réunion pink pigeon	<i>Nesoenas duboisi</i> Roths- child, 1907a	Nesoenas duboisi	_	†FE	-
Mauritius turtle dove	Nesoenas cicur HUME, 2011	Nesoenas cicur	†FE	_	_
Réunion turtle dove	<i>Streptopelia picturata</i> Tem- MINCK, 1813	Nesoenas aff. picturata	_	†FE?	-
Rodrigues turtle dove	<i>'Columba' rodericana</i> (Milne-Edwards, 1874)	Nesoenas rodericana	-	_	†FE
Mauritius Blue Pigeon	<i>Columba nitidissima</i> Sco- POLI, 1786	Alectroenas nitidissima	†FSE	_	-
Rodrigues blue pigeon	<i>Alectroenas payandeei</i> Hume, 2011	Alectroenas payandeei	-	_	†FE
Mascarene parrot	<i>Psittacus mascarinus</i> Lin- NAEUS, 1771	Mascarinus mascarinus	-	†FSE	-
Broad-billed parrot or raven parrot	Psittacus mauritianus Owen, 1866b	Lophopsittacus mauri- tianus	†FΕ	_	-
Rodrigues parrot	<i>Psittacus rodericanus</i> Milne- Edwards, 1867a	Necropsittacus roderi- canus	-	_	†FE
Thirioux's grey parrot	Lophopsittacus bensoni Holyoak, 1973	Psittacula bensoni	†FΕ	_	_

TABLE 1. (continued).

Common name	Original Latin name & authority	Current Latin name	Mauritius	Réunion	Rodrigues
Echo parakeet	Palaeornis echo Newton & Newton, 1876	Psittacula echo	FE	_	_
Rodrigues parakeet	Palaeornis exsul Newton, 1872	Psittacula exsul	_	_	†FSE
Commerson's lizard- owl	<i>Strix sauzieri</i> Newton & Gadow, 1893	Mascarenotus sauzieri	†FE	_	_
Gruchet's or Réunion lizard-owl	<i>Mascarenotus grucheti</i> Mourer-Chauviré, Bour, Moutou & Ribes, 1994	Mascarenotus grucheti	_	†FE	_
Rodrigues lizard-owl	Strix (Athene) murivora Milne-Edwards, 1874	Mascarenotus muriv- orus	_	_	†FE
Mascarene swiftlet	<i>Hirundo francica</i> Gmelin, 1879	Collocalia francica	Ind	Ind	_
Mauritius cuckoo- shrike	<i>Oxynotus typicus</i> Hartlaub, 1865	Coracina typica	FE	_	-
Réunion cuckoo-shrike	Oxynotus newtoni Pollen, 1866	Coracina newtoni	_	Е	-
Mascarene flycatcher	<i>Muscicapa bourbonnensis</i> Statius Müller,1776	Terpsiphone bourbon- nensis	Е	Е	-
Mascarene swallow	Hirundo borbonica Gmelin, 1789	Phedina borbonica borbonica	Ind	Ind	IndV
Mauritius bulbul or merle	<i>Hypsipetes olivaceus</i> Jardine & Selby, 1835	Hypsipetes olivaceus	FE	_	-
Réunion bulbul or merle	<i>Turdus borbonicus</i> Forster, 1781	Hypsipetes borbonicus	_	Е	-
Rodrigues bulbul		Hypsipetes sp.	_	_	†FE
Rodrigues warbler	Drymoeca rodericanus New- TON, 1865	Bebrornis (Acrocepha- lus) rodericanus	_	_	FE
Mauritius olive white- eye	Zosterops chloronothos VIEILLOT, 1817	Zosterops chloronothos	FE	_	-
Réunion olive white- eye	<i>Certhia olivaceus</i> Linnaeus, 1766	Zosterops olivaceus	-	Е	-
Mauritius grey white- eye	<i>Motacilla borbonica</i> For- ster, 1781 (see http://www. zoonomen.net)	Zosterops borbonicus	FE	_	_
Réunion grey white- eye	<i>Motacilla mauritianus</i> Gme- LIN, 1789	Zosterops mauritianus	_	Е	-
Réunion crested star- ling or huppe	Upupa varia Boddaert, 1783	Fregilupus varius	_	†FSE	_
Mauritius starling		Sturnidae	†FE	_	_
Rodrigues starling	<i>Necropsar rodericanus</i> Günther & Newton, 1879	Necropsar rodericanus	_	_	†FE
Réunion stonechat	<i>Muscicapa tectes</i> Gmelin, 1789	Saxicola tectes	_	Е	-
Mauritius fody	Emberiza rubra Gmelin, 1789	Foudia rubra	FE	_	_
Réunion fody	<i>Foudia delloni</i> Cheke & Hume, 2008	Foudia delloni	-	Е	-
Rodrigues fody	Foudia flavicans Newton, 1865	Foudia flavicans	_	_	FE

Herons and Egrets (Ardeidae)

Early travelers to the Mascarenes mentioned a number of herons, but the accounts are extremely vague and it is very difficult to interpret the descriptions. Subfossil remains confirm that three endemic species once inhabited the islands (ROTHSCHILD 1907a, b; CHEKE 1987); however, NEWTON & GADOW (1893) mention six species of heron, all collected from the Mare aux Songes. My analysis of these latter specimens shows that only three were correctly identified as herons (see below); whereas three are not herons at all (see *Phalacrocorax africanus, Alopochen mauritianus* and *Circus maillardi*).

Nycticorax mauritianus — The genus Nycticorax (night herons) gave rise to three endemic Mascarene species, all now extinct. LEGUAT (1708) mentioned 'flights of bitterns' in 1693 on Mauritius, which were probably referable to the Mauritian night heron, N. mauritianus, and it is generally assumed that the birds disappeared shortly after this date (CHEKE & HUME 2008; HUME & WALTERS 2012). The Mauritian night heron has often been cited as being flightless, but this was certainly not the case. Although the tarsometatarsus is robust and indicative of a more terrestrial mode of life, a humerus collected from the Mare aux Songes in 1865, but erroneously attributed to great white egret, Ardea alba LINNAEUS, 1758 by NEWTON & GADOW (1893), is morphologically more similar to Nycticorax and equivalent in size of that of any volant Nycticorax species (HUME unpubl. data).

Nycticorax duboisi — DUBOIS (1674) gave the best account of a night heron from Réunion, a species now confirmed by skeletal remains (COWLES 1994), but appears to have described a juvenile (CHEKE 1987; MOURER-CHAUVIRÉ *et al.* 1999). Night herons were not mentioned again after DUBOIS's account (HUME & WALTERS 2012). This was the largest Mascarene species, and like the Mauritian bird, it showed no reduction in wing elements (MOURER-CHAUVIRÉ *et al.* 1999).

Nycticorax megalocephalus — The Rodrigues night heron was a robust species, with a stout, straight bill and robust legs (CowLes 1987). It was described by TAFFORET in 1725–26 as a species reluctant to fly (HUME & WALTERS 2012). The skeletal morphology confirms that this species

was evolving towards flightlessness, but it was still capable of flight. During the Transit of Venus expedition in 1761–3, the astronomer Alexandre-Gui Abbe PINGRÉ made a detailed survey of the Rodrigues fauna (NAGAPEN 2004), noting that the herons had by this time disappeared. An incomplete associated individual, which included the cranium and jaws, was discovered in Caverne Poule Rouge in 2006 (HUME unpubl. data).

Butorides striatus — Green-backed herons are resident on all of the Mascarene Islands. They are considered to be of the Javan race, *B. s. javanicus* (RIPLEY 1969), and thought to be a recent colonist to the islands (CHEKE & HUME 2008). However, I have identified subfossil remains from Mare aux Songes deposits on Mauritius, and I collected subfossil remains from Caverne Dora on the Plaine Corail, Rodrigues. *Buterides striatus* is a complex group, which not only has a large number of subspecies, but also exhibits extensive individual variation. It is possible that the Mascarenes may once have had an endemic species or subspecies of green-backed heron, but further work is needed before any conclusions can be made.

Egretta dimorpha — The dimorphic egret is common on Madagascar and vagrant to other Indian Ocean Islands (SINCLAIR & LANGRAND 2004), and once occurred on Mauritius and Réunion (CHEKE & HUME 2008). WEST-ZANEN (1648) mentioned them in 1602 on Mauritius, whilst DUBOIS (1674) and FEUILLEY (1705) described them on Réunion. Dimorphic egrets appear to have disappeared sometime during the 18th century. NEWTON & GADOW (1893) attributed a tarsometatarsus collected at the Mare aux Songes as belonging to '*Ardea ardesiaca'*, but I found that it is referable to *E. dimorpha*, this being the only known subfossil element of this species.

Tropicbirds (Phaethontidae)

Phaethon rubricauda — The red-tailed tropic bird remains fairly common on Mauritius (SIN-CLAIR & LANGRAND 2004), breeding on Round Island off the north coast. It is a rare vagrant to Réunion (PROBST 1997) and, although scarce, still inhabits the islets within the lagoon surrounding Rodrigues, and was reported to have bred on the cliffs of Cascade Victoire in 1967 (STAUB 1973; 1976). No subfossil remains of *P. rubricauda* have yet been identified on the Mascarenes.

Phaethon lepturus — The white-tailed tropic bird is widely distributed throughout the Mascarenes, and it is the most abundant subfossil bird species found in cave deposits on Rodrigues (HUME 2005); adults, juveniles and eggs are equally represented. After a period of decline on Rodrigues, it is now recovering in numbers, and live birds and occasional fresh corpses are encountered in and around the cave sites.

Frigate-birds (Fregatidae)

Fregata minor/Fregata ariel — Frigate-birds have a wide Indo-Pacific distribution and occur on oceanic islands throughout the Indian Ocean (SINCLAIR & LANGRAND 2004). Both species are rare vagrants to Réunion (BARRÉ et al. 1996). Two species are thought to have once bred on Mauritius and Rodrigues, the greater frigate-bird, Fregata minor, and the lesser frigate-bird, F. ariel (CHEKE 1987). On Mauritius, they were once resident breeders, and a frigate-bird is shown in an engraving depicting Dutch activities ashore in 1598 (HET TVVEEDE BOECK 1601). Both species had all but disappeared by the 1850s; the last confirmed sightings were on Round Island, Mauritius (E. NEWTON 1861; CHEKE 1987). On Rodrigues, frigates occurred on many of the islets within the lagoon; Pingré reported them as common (CHEKE 2001; NAGAPEN 2004), but it appears that they only bred on Ile aux Fregate (CHEKE 1987). Frigate-birds had probably ceased to breed on Rodrigues by c. 1850 and were considered rare in 1916 (BERTUCHI 1923). They do, however, turn up as rare vagrants within the Mascarenes (CHEKE 1987). Probably due to their tree-top nesting preferences and extremely fragile and lightweight skeleton, no subfossil remains of frigate-birds have been discovered in the Mascarenes.

Gannets and boobies (Sulidae)

Sula sula — The red-footed booby occurs yearround on Mauritius but probably never bred there (CHEKE 1987, 2001). They do not occur on Réunion (PROBST 1997). The islets off Rodrigues, particularly Ile aux Fregate, once harboured large colonies of boobies, and at least one species, dark phase red-footed booby, *Sula sula*, was a resident breeder (CHEKE 2001). The population is now extirpated, being last reported in 1916 (BERTUCHI 1923; CHEKE 1987, 2001). No *S. sula* bones have yet been identified in the Mascarenes.

Sula dactylatra — The masked booby is vagrant to Réunion and still breeds on Serpent Island off Mauritius, the only known breeding site in the Mascarenes (STAUB 1976; CHEKE 2001), but being a ground nesting bird it is vulnerable to disturbance. As yet, no subfossil remains of this species have been found in the Mascarenes.

Papasula abbotti — Abbott's booby is now confined to Christmas Island, Indian Ocean, the only known breeding population, but colonies also once occurred on Assumption Island and on the Mascarenes. It is also a rare vagrant to the Pacific (PRATT et al. 2009). Abbott's booby was mentioned by a number of observers on Rodrigues during the 18th century (BOURNE 1976; CHEKE 1987, 2001), but was last recorded in 1761 by Pingré (Cheke & Hume 2008). Bourne (1976) confirmed the presence of Abbott's booby on Mauritius from a complete humerus and ulna, collected in the Mare aux Songes. I discovered a proximal humerus, which was mis-identified as solitaire Pezophaps solitaria, from Rodrigues cave deposits. Comparison of the Mare aux Songes and Rodrigues specimens with Christmas Island birds indicates that the Mascarene population is distinct. This may also be the case with the Assumption birds (HUME unpubl. data).

Cormorants (Phalacrocoracidae)

Phalacrocorax (Microcarbo) africanus — Cormorants were reported on Réunion during the early years of settlement; DUBOIS (1674) and FEUILLEY (1705) in particular gave good descriptions. They were encountered on the lakes, and when young were considered good to eat (HUME & WALTERS 2012). They were not recorded again however and presumably died out in the early 18th century. Although not mentioned in early accounts, cormorant subfossil remains have been excavated from the Mare aux Songes. OLSON (1975) referred them to the reed cormorant Phalacrocorax africanus, a wide ranging African species that is represented on Madagascar by the race pictilis BANGS, 1918. However, my analysis of the specimens indicates that it was a smaller taxon, and may represent a new, but extinct subspecies (HUME & WALTERS 2012). By contrast, an ulna collected from the Mare aux Songes and erroneously referred to *Ardea alba* LINNAEUS, 1758 (NEWTON & GADOW 1893), is most similar to *P. africanus pictilis* (HUME unpubl. data).

Darters and Anhingas (Anhingidae)

Subfossil remains obtained from the Mare aux Songes were described as an endemic anhinga, *Plotus nanus* (NEWTON & GADOW, 1893), related to the Madagascar species *A. rufa* DAUDIN, 1802. OLSON (1975) re-examined the material and concluded that it was in fact referable to the African Reed Cormorant *Phalacrocorax* (*Microcarbo*) *africanus* (see below).

Hawks and Falcons (Accipitridae)

Birds of prey have populated many island groups throughout the Indian Ocean and far-ranging migrants regularly visit the Mascarenes (SINCLAIR & LANGRAND 2004). Two genera are certainly known from Réunion and Mauritius, *Circus* and *Falco*, while a possible third genus remains indeterminate (MOURER-CHAUVIRÉ *et al.* 1999).

Falco punctatus — The Mauritius kestrel was once considered the most endangered bird in the world, with numbers down to six birds in 1974 (JONES 1987). Due to intensive captive breeding and conservation efforts, by 2005 numbers increased to an estimated 800–1000 individuals (JONES in CHEKE & HUME 2008), but this estimate was prematurely optimistic. The population has dropped to <400 individuals and continues to decline (CADE 2008). A few subfossil elements have been collected from both the Mare aux Songes and from caves beneath Le Pouce Mountain.

Falco duboisi — A morphologically distinct species of kestrel, *F. duboisi*, once inhabited Réunion, and was described from subfossil material collected in 1974 (CowLes 1994). In 1671–2 it was reported to 'do harm to the fowls of the inhabitants and the game of the island' by DUBOIS (1674) and was persecuted accordingly, but this was its only record from life, so the date of its extinction is unknown (HUME & WALTERS 2012). The Mauritius kestrel has short, rounded wings, which is indicative of a forest inhabitant (JoNES 1987), whereas the Réunion kestrel was more similar to the Eurasian kestrel complex, which are open habitat specialists (MOURER-CHAUVIRÉ et *al.* 1999).

Circus maillardi — Two species of Circus harrier have been described from the Mascarenes. However, that described from subfossil material on Mauritius as Circus alphonsi Newton & GADOW, 1893, has been shown by MOURER-CHAUVIRÉ et al. (2004) to be conspecific with the Réunion Harrier, C. maillardi, which is extant but endangered on Réunion. On Mauritius, the species is known from subfossil remains collected from the Mare aux Songes and cave deposits around Le Pouce Mountain (NEWTON & GADOW 1893; RIJSDIJK et al. 2009), including an ulna formerly attributed to Nycticorax mauritianus that I have shown is referable to C. maillardi; it is also briefly mentioned in the account of Cornelis MATELIEFF DE JONGE in 1606 (BARNWELL 1948).

TABLE 2. List of species that almost certainly once existed, but lack supporting fossil evidence. This category of 'hypothetical' taxa is restricted to Réunion, primarily due to the paucity of subfossil remains of certain avian orders on that island.

Common name	Original Latin name & authority	Current Latin name	Mauritius	Réunion	Rodrigues
Emerillon		Falco? sp.	-	Х	-
Oiseaux bleu	Cyanornis coerulescens Sélys-Longchamps, 1848	Cyanornis (Porphyrio) coerulescens	-	Х	-
Réunion blue pigeon		Alectroenas sp.	-	Х	_
Réunion ring-necked parakeet	<i>Psittacus eques</i> Boddaert, 1783	Psittacula eques	-	Х	-
Réunion grey parrot		Psittacula aff. bensoni	-	Х	-
Réunion red and green parrot	<i>Necropsittacus' borboni- cus</i> Rothschild, 1907b	Genus indeterminate	_	Х	-

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No Réunion subfossil material is known. Why the Réunion population has survived, whereas the Mauritius birds disappeared in the early years of human settlement, remains unclear.

Small falcon — Réunion. An enigmatic species called an 'Emerillon (=merlin)' was described by DUBOIS (1674) as 'although small, do not fail to carry away chickens and eat them' (MOURER-CHAUVIRÉ *et al.* 1999). CHEKE (1987) suggested that this description was referable to *Falco duboisi*, but kestrels had already been mentioned in DUBOIS's account. The Emerillon may have been a migratory *Falco* species or an endemic small hawk that is now extinct.

Rails and coots (Rallidae)

Rails have colonised almost every oceanic island archipelago throughout the world. At least five genera formerly occurred on the Mascarenes, and two of these, the Mauritius red rail *Aphanapteryx bonasia*, and Rodrigues rail *Erythromachus leguati*, must have been isolated for some time; their relationships with other rails are now difficult to determine (OLSON 1977; LIVEZEY 1998, 2003). A sixth genus, *Gallinula*, which still occurs on Mauritius and Réunion, may have been a recent arrival (CHEKE & HUME 2008).

Aphanapteryx bonasia — The monotypic genus Aphanapteryx is characterised by hair-like plumage, a long de-curved bill, vestigial wings and strong, robust legs. The Mauritius red rail, A. bonasia, appears to have been an opportunist omnivore and was able to survive two centuries of anthropogenic changes (HUME & WALTERS 2012). However, the introduction of cats in the late 17th century proved disastrous, and the rails were not seen again after 1693 (CHEKE & HUME 2008). The Mauritius red rail was originally described from illustrations and accounts (Sélys-Longchamps 1848), but the discovery of subfossil remains from the Mare aux Songes allowed MILNE-EDWARDS (1868) to correctly assign it to the Rallidae. Subfossil remains have also been collected in a number of widespread cave localities, which includes a complete associated individual collected by THIRIOUX somewhere around Le Pouce Mountain and a partially associated individual from a cave near Vieux Grand Port in the southeast.

Erythromachus leguati — The Rodrigues rail is sufficiently distinct from *A. bonasia* in a number of characteristics to warrant generic separation (OLSON 1977; MOURER-CHAUVIRÉ *et al.* 1999; HUME & WALTERS 2012). It was reported to be common in 1691–3 (LEGUAT 1708) and in 1725–6 by TAFFORET (HUME & WALTERS 2012), but PIN-GRÉ in 1761 (HUME & WALTERS 2012), but PIN-GRÉ in 1761 (HUME & WALTERS 2012) stated that the species was by then extinct. A large series of subfossil remains collected by colleagues and I in caves on the Plaine Corail exhibit a great size variation, almost certainly due to sexual dimorphism. An incomplete but associated individual, which includes a complete skull and jaws, was collected in Caverne Poule Rouge in 2005.

Dryolimnas augusti — The volant nominate white-throated rail Dryolimnas cuvieri PUCHERAN, 1845 is widely distributed in Madagascar, where it is reasonably common (SINCLAIR & LANGRAND 2004). Interestingly, the type, a gravid female collected on Mauritius (PUCHERAN 1845), may have been a vagrant. There are two closely related subspecies, the flightless Aldabran rail, D. c. aldabranus (GÜNTHER, 1879), from Aldabra atoll, which holds the distinction of being the last surviving Indian Ocean flightless bird, and the recently extinct Assumption Island rail, D. c. abbotti RIDGWAY, 1894, which had reduced flying capabilities. A second species, only tentatively placed in Dryolimnas, has recently been described from fossil remains collected in the Caverne de la Tortue, Réunion (MOURER-CHAU-VIRÉ et al. 1999). This Réunion rail D. augusti was morphologically similar, although larger, than the Aldabran species and was probably also flightless. Dubois (1674) mentioned a 'wood rail' in his list of species, and this is almost certainly referable to the Réunion rail (MOURER-CHAUVIRÉ et al. 1999).

Dryolimnas sp. — Mauritius. Cowles (1987) identified Dryolimnas material collected from the Mare aux Songes, which had previously been ascribed to the common moorhen Gallinula chloropus LINNAEUS, 1758 (NEWTON & GADOW 1893). However, he referred the material to nominate D. cuvieri. I identified more Dryolimnas material from a collection made by Thirioux in caves around Le Pouce Mountain, which shows that an endemic, flightless Dryolimnas once occurred on Mauritius.

Cyanornis (Porphyrio) coerulescens — The

most enigmatic of all Mascarene rails is the 'Oiseau bleu,' a bird that once occurred on the Plaine des Cafres, Réunion. They were mentioned on a number of occasions by trustworthy observers and last reported around the middle of the 18th century (CHEKE & HUME 2008). Their colour was described as blue with red beak and legs (e.g., Dubois 1674), and they were considered good game and, although able to fly, could easily be caught and killed with sticks (CHEKE & HUME 2008). No subfossil remains have yet been found to resolve their affinities, but the oiseau bleu is generally considered to represent a large Porphyrio gallinule (HUME & WALTERS 2012), a genus which occurs on Madagascar (SINCLAIR & LANGRAND 2004). No subfossil remains are known from the rich Mare aux Songes deposits or from the THIRIOUX montane collections, which suggest that Mauritius lacked suitable habitat for this taxon.

Gallinula chloropus — The common moorhen is found on a number of western Indian Ocean islands, including Mauritius and Réunion (SINCLAIR & LANGRAND 2004). The Mascarene populations are generally treated as part of *G. c. pyrrhorrhoa* A. NEWTON, 1861, that also occurs on Madagascar and the Comoro Islands, and appear to be of recent origin (CHEKE & HUME 2008). No subfossil remains of *Gallinula* have been identified on the Mascarenes.

Fulica newtoni — A coot of the genus *Fulica* was once found on Mauritius and Réunion. Despite some suggestions that *F. newtoni* was flightless, there is no reduction in the pectoral elements. Furthermore, the birds from Mauritius and Réunion are undifferentiated, indicating that the species was clearly able to fly between the islands (MOURER-CHAUVIRÉ *et al.* 1999; CHEKE & HUME 2008). Both populations had disappeared by the end of the 17th century (HUME & WALTERS 2012). *F. newtoni* was described from subfossil remains from the Mare aux Songes (MILNE-EDWARDS 1867), and skeletal elements were collected by KERVAZO in the Grotte des Premiers Française on Réunion (CowLes 1994).

Button-Quails (Turnicidae)

It appears that there was once an indigenous population of button-quails on Réunion, which were mentioned in a number of accounts, but appeared to have died out around the 1670s (CHEKE 1987). It is very likely that these button-quails were *Turnix nigricollis* (GMELIN, 1789), a native of Madagascar. Madagascar button-quails were introduced around 1714 on Réunion and possibly during the 1830s on Mauritius (CHEKE & HUME 2008); they still occur on Mauritius and Réunion today (SINCLAIR & LANGRAND 2004). No subfossil remains have been found on Réunion, whereas a few post-cranial elements were collected by THIRIOUX around Le Pouce Mountain.

Waders (Scolopacidae)

A number of waders are regular migrants to the Mascarenes, but only two are identifiable from early accounts and only one from the fossil record.

Numenius phaeopus — The whimbrel is a common migrant to the Mascarenes, and appears to have been regularly hunted on Mauritius in the past. The only evidence of this species in the fossil record is an ulna collected in the Mare aux Songes, Mauritius, which was originally assigned to a *Podiceps* sp. by NEWTON & GADOW (1893) and later formally described as *P. gadowi* (1893) and later formally described as *P. gadowi* HACHISUKA, 1953. COWLES (1987) re-identified this specimen and correctly assigned it to *Numenius phaeopus*. A tarsometatarsus was also collected in the Grotte des Premiers Française on Réunion (MOURER-CHAUVIRÉ *et al.* 1999).

Numenius arquata — The curlew is a less frequent migrant to the Mascarenes, and was also regularly hunted in the past. No subfossil remains of this species have yet been identified.

Terns (Stercorariidae)

A number of terns breed on off-shore islands on the Mascarenes, but all are unknown in the fossil record, so they are mentioned here only for completeness. The populations of common noddy *Anous stolidus* (LINNAEUS, 1758), lesser noddy *Anous tenuirostris* (TEMMINCK, 1823), sooty tern *Sterna fuscata* (LINNAEUS, 1766), bridled tern *Onychoprion anaethetus* (SCOPOLI, 1786) and fairy tern *Gygis alba* (SPARRMAN, 1786) were variously mentioned in early accounts as being extremely abundant, especially on Rodrigues (CHEKE & HUME 2008), but are now much reduced in numbers.

Pigeons and doves (Columbidae)

Pigeons and doves, including the dodo and solitaire, are mentioned in almost all early accounts that relate to the Mascarene fauna. All describe their inherent tameness and the ease with which they could be caught, but few provide descriptive details. Only one species, *Nesoenas mayeri*, of at least 12 endemic pigeons and doves (HUME 2011), survives today.

Raphus cucullatus — The dodo has been the subject of more debatable literature than any other bird (HUME 2006). It was first mentioned in 1599 and first illustrated in 1600 (HUME 2006). but became extinct sometime between 1662 (CHEKE 1987) and 1693 (HUME et al. 2004). MtDNA analysis has shown that the dodo and solitaire Pezophaps solitaria are monophyletic and have a sister group relationship to the Nicobar pigeon Caloenas nicobarica (PEREIRA et al. 2007; SHAPIRO et al. 2002). Almost all of the known subfossil remains were excavated from the Mare aux Songes, but THIRIOUX collected an associated individual and a partially associated individual from undisclosed caves in the centre of the island. More recently, a complete but badly degraded specimen was excavated at Bois Cheri, in the central uplands (MIDDLETON & HUME In press), and individual elements have been collected from caves at Vieux Grand Port, La Prairie, Baie du Cap and Roches Noires and from a marsh at Flacq (JANOO 2005; HUME et al. 2009). According to the fossil evidence, the dodo was once widely distributed around Mauritius, but predominantly confined to the lowlands. This may also represent a bias, as fossil depositional environments are more numerous in the lowlands and the lowland cave and marsh deposits are more conducive to bone preservation (HUME 2005). Juvenile dodo remains are incredibly rare; only one tarsometatarsus collected by THIRIOUX from an unspecified cave/boulder scree deposit in the valleys around Le Pouce (photographed and now lost (HUME 2006)), and a fragment from a cave at La Prairie have been collected.

Pezophaps solitaria — The solitaire was the closest relative of the dodo and endemic to

Rodrigues, but differed markedly in morphology. It was considered to be common when first described (LEGUAT 1708; TAFFORET in HUME & WALTERS 2012), but had disappeared by the 1760s. The solitaire is known from a femur collected at Anse Mourouk and thousands of skeletal elements, including associated individuals, from caves on the Plaine Corail. It exhibited the greatest sexual dimorphism known in any neognathous bird (LIVEZEY 1993), and both sexes were extremely aggressive when defending their territories (HUME & STEEL 2013). However, not a single juvenile specimen has yet been identified.

Columba thiriouxi—A small species of pigeon, tentatively referred to typical *Columba* (HUME 2011), disappeared sometime after 1730 (HUME & WALTERS 2012). It is known from subfossil cave deposits collected around Le Pouce Mountain and Plain des Roches. The short, broad tarsometatarsus suggests that it was an arboreal species.

Endemic *Nesoenas* pink pigeons were confined to Mauritius and Réunion, whereas *Nesoenas* turtle doves once occurred on all three Mascarene Islands. All but the Mauritius pink pigeon *Nesoenas mayeri* had disappeared during the early 18th century. Introductions of Madagascar turtle doves *Nesoenas picturata* (TEMMINCK, 1813) took place on Mauritius and Réunion after the extinction of the native birds, and present populations of *N. picturata* are all introduced. This Madagascar species differs from the endemic *Nesoenas* turtle doves in a number of osteological details (see HUME 2011), and is almost certainly unknown in the fossil record.

Nesoenas mayeri — The pink pigeon is the only surviving Mascarene columbid and confined to Mauritius. It had been reduced to less than 25 birds in the 1970s, but a successful captive-breeding and re-introduction programme has increased the population to 350+ individuals today (JONES in CHEKE & HUME 2008). It is the commonest subfossil species found in cave deposits, but markedly less so in the Mare aux Songes marsh (HUME 2011).

Nesoenas duboisi — The Réunion pink pigeon was described by ROTHSCHILD (1907a, b) based on the account of DUBOIS (1674), the only person to record it in life. Humeri referable to this taxon discovered in Grotte des Premiers Française and Grotte de l'Autel are larger than *N*. *mayeri* (MOURER-CHAUVIRÉ *et al.* 1999), a closely related species.

Nesoenas cicur — The Mauritius turtle dove is known from subfossil remains collected at the Mare aux Songes and cave deposits situated in the valleys of Le Pouce Mountain and at Vieux Grand Port (HUME 2011). It became extinct sometime after 1730. The Mauritius turtle dove had comparatively robust pelvic elements and reduced pectoral elements, so was probably more terrestrial than other *Nesoenas* pigeons.

Nesoenas aff. *picturata* — Two *Nesoenas* subfossil elements collected in the Grotte "au sable" on Réunion (MOURER-CHAUVIRÉ *et al.* 1999) may be referable to *N. cicur* or a closely related species (HUME 2011).

Nesoenas rodericana — The Rodrigues turtle dove is known from early accounts and from cave deposits collected on the Plaine Corail (Hume 2011). It was a small species, with a distinct sternum, and disappeared between 1726 and 1761, due to rat predation and deforestation (Hume & WALTERS 2012). Partially associated individuals were discovered in Caverne Bambara II in 2006, and Caverne l'Affouche in 2013.

Alectroenas nitidissima — Despite being persecuted for over two centuries, the Mauritius blue pigeon was still comparatively numerous at the end of the 18th century. However, due to severe deforestation, it had disappeared by 1837 (HUME 2011; HUME & WALTERS 2012). It is known from three skins, the most recent taken in 1826 (MILNE-EDWARDS & OUSTALET 1893), and a few subfossil remains collected from the Mare aux Songes and caves around Le Pouce and Roches Noires (HUME 2011).

Alectroenas sp. — It seems probable that an Alectroenas once occurred on Réunion (HUME 2011), as a bird of this description was briefly mentioned by DUBOIS (1674) and BONTEKOE (1650), but no skeletal remains have been found to confirm its affinities.

Alectroenas payandeei — The Rodrigues blue pigeon was never mentioned by any visitors to the island. It is known from a single but distinct tarsometatarsus, collected in Caverne Poule Rouge on the Plaine Corail (HUME 2011).

Parrots (Psittacidae)

It is difficult to determine how many species

of parrot once inhabited the Mascarenes (HUME 2007), but at least seven taxa were present on the islands, with a further two awaiting confirmation from the fossil record. Like the columbids, almost every early account mentions them, but few provide any details. They were rapidly hunted to extinction, long before any scientific analysis could take place. All Mascarene parrots are now extinct save the echo parakeet *Psittacula echo* (NEWTON & NEWTON, 1876) of Mauritius.

Mascarinus mascarinus — The Mascarene parrot is known from two skins, both collected during the 18th century, and from a few subfossil elements excavated in caves on Réunion (MOURER-CHAUVIRÉ et al. 1999). DUBOIS (1674) gave a good description of this species in 1671-72 and a few live birds survived the journey to France (BRISSON 1760; MAUDUYT 1784). The much repeated 1834 date of extinction (HAHN 1834) is unfounded; the Mascarene parrot had almost certainly disappeared by c. 1800 (HUME 2007). Analysis of skeletal material and similarities in colouration strongly suggest a direct relationship with southeast Asian Psittaculini parrots (Mourer-Chauviré et al. 1999; Hume 2007), but mtDNA analysis, according to KUNDU et al. (2012), embedded Mascarinus within Coracopsis nigra (LINNAEUS, 1758), the lesser vasa parrot of Madagascar and nearby islands. However, this result has been questioned (JOSEPH et al. 2012).

Necropsittacus rodericanus — The Rodrigues parrot was described as a big-headed, long-tailed bird that frequented the southern islets off Rodrigues, returning to the mainland only to drink water (HUME 2007). Pingré listed *N. rodericanus* as very rare in 1761 and this was the last time it was mentioned (HUME & WALTERS 2012). Subfossil remains are scarce, although cranial and post-cranial specimens have been recovered from unnamed caves on the Plaine Corail. Colleagues and I discovered a rostrum, humerus, and tibiotarsus in Caverne Tortue in 2008.

Lophopsittacus mauritianus — The raven parrot or broad-billed parrot, which was last recorded in 1673–4, had developed huge jaws for cracking the hard nut shells of palms and other forest trees (HUME 2007, contra HOLYOAK 1971), and exhibited the greatest sexual dimorphism known in any parrot (HUME 2007). Despite statements to the contrary (*e.g.*, HACHISUKA 1953), there is no evidence to suggest that this species was flightless (HUME 2007), but it was probably poorly volant. It is known from numerous subfossil remains from the Mare aux Songes, Mauritius, with a preponderance of mandibles and tibiotarsi (HUME 2005), and also from a few specimens collected in caves around Le Pouce Mountain.

At least two species of *Psittacula* parakeet colonised the Mascarenes. A *Psittacula eupatria* (LINNAEUS, 1766) derivative, *P. wardi* (NEWTON, 1867), once occurred on the Seychelles, with probable derivatives on Mauritius (*P. bensoni*), Réunion (*P.* aff. *bensoni*/ red and green parrot) and possibly Rodrigues (*P. exsul*) (HUME 2007). A second colonisation event involved *P. krameri* (SCOPOLI, 1769), with derivatives on Mauritius (*P. echo*) and on Réunion (*P. eques*) (GROOMBRIDGE *et al.* 2004).

Psittacula bensoni — THIRIOUX's grey parrot was a long-tailed, large-headed species, and a probable derivative of the *Psittacula 'eupatria'* group (HUME 2007). It was considered to be one of the commonest species on Mauritius during the early 18th century, but had disappeared by *c*. 1760 (HUME 2007; HUME & WALTERS 2012). Subfossil remains are rare. It is known from cave deposits collected by THIRIOUX from the valleys around Le Pouce Mountain (HUME 2007) and from a few skeletal specimens from the Mare aux Songes (RIJSDIJK *et al.* 2009).

Psittacula aff. *bensoni* — DUBOIS (1674) and COSSIGNY (1732–55) mentioned a grey parrot on Réunion, which may have been conspecific with *P. bensoni*. However, no skeletal remains have been found to determine its relationships. It was last recorded in *c*. 1730 (CHEKE & HUME 2008).

Psittacula exsul — The Rodrigues parakeet is known from two skins collected in the early 1870s (NEWTON 1875), just prior to the species becoming extinct. There appear to have been two colour morphs (green and blue), of which only the blue morphs were collected. Subfossil remains are rare, but morphometric analysis and one contemporary description suggest that this species may have been derivative of the *Psittacula 'eupatria'* group (HUME 2007).

Psittacula echo — The echo parakeet, the only surviving psittaciform in the Mascarenes, was described in the 1980s as the world's rarest parrot, with a population of less than a dozen

birds (FORSHAW 1989). It has now recovered to some 350 mature individuals (JONES in CHEKE & HUME 2008). Large numbers of subfossil remains have been excavated in caves around Le Pouce Mountain and Plaine des Roches, including juveniles (HUME 2007), but its remains are rare in the Mare aux Songes deposits.

Psittacula eques — The Réunion parakeet is known only from a number of paintings and accounts (HUME 2007) and, putatively, one skin (JONES 1987; but see CHEKE & HUME 2008). Despite the survival of *Psittacula echo* on Mauritius, *P. eques* disappeared early in Réunion's history, being last reported around 1730 (HUME & WALTERS 2012). Pending confirmation from fossil remains, it may be conspecific with *P. echo*.

Réunion red and green parrot. Genus indeterminate. This enigmatic bird, which was reported only once, has caused much taxonomic confusion. DUBOIS (1674), whose observations can be trusted, described a green parrot with head, wings and tail the colour of fire. It was formerly described as '*Necropsittacus' borbonicus* ROTHS-CHILD, 1907b, based on the assumption that it was related to *N. rodericanus* of Rodrigues (ROTH-SCHILD 1907a), but ROTHSCHILD confused the early literature (HUME 2007). It is possible that DUBOIS was describing an endemic *P. 'eupatria'* species on Réunion. The colouration, apart from the red tail, is typical of *P. eupatria* (HUME 2007).

Owls (Strigidae)

Owls of the genus *Otus* occur on a number of Indian Ocean islands (FUCHS *et al.* 2008) and it is from this genus that the endemic Mascarene genus *Mascarenotus* was derived (MOURER-CHAUVIRÉ *et al.* 1994). The Mascarene species were characterised by large size and robust, long legs (NEWTON & GADOW 1893; MOURER-CHAUVIRÉ *et al.* 1994), presumably adaptations for predation of reptiles and small birds. The Mascarene lizard-owls are known from descriptions, one drawing and a few subfossil remains.

Mascarenotus sauzieri — The Mauritian lizard-owl was a large eared owl with bare tarsi. A drawing by Jossigny, reproduced in Ousta-LET (1897), is the only known illustration of the genus. One individual was described in detail by DESJARDINS (1837), the specimen of which was lost during a cyclone in the 1850s (CHEKE & HUME 2008), while a few others were reported around the same time (CHEKE & HUME 2008). *M. sauzieri* appears to have required large trees for nesting and roosting, and disappeared due to extensive deforestation. CLARK (1859) stated that at the time of writing they had become extinct after being formerly plentiful. THIRIOUX collected subfossil remains from cave deposits around Le Pouce and Plaine des Roches, which includes some partially associated material. I collected a complete pelvis in 2007 in Kanaka Cave, Bois Cheri.

Mascarenotus grucheti — Owls were never reported historically on Réunion, but subfossil remains confirm that a species once occurred there (MOURER-CHAUVIRÉ *et al.* 1994, 1999). It differed from *M. sauzieri* in having slightly more reduced wing elements (MOURER-CHAU-VIRÉ *et al.* 2006).

Mascarenotus murivorus — The Rodrigues lizard-owl was mentioned by LEGUAT (1708) and

TAFFORET (HUME & WALTERS 2012), the latter stating that the small brown owls fed on lizards and birds and lived almost exclusively in trees. PINGRÉ in 1761 never reported them, so they presumably disappeared sometime between the visits of TAF-FORET in 1725–26 and PINGRÉ (HUME & WALTERS 2012). Subfossil remains are rare in caves at the Plaine Corail, which suggests that they were not using these areas for roosting or breeding.

Swifts (Apodidae)

Collocalia francica — The Mascarene swiftlet has decreased in numbers on Mauritius, but it is still common on Réunion (SINCLAIR & LANGRAND 2004). Fresh skeletal specimens are comparatively numerous on Mauritius, but no subfossil remains have been identified from either island. Despite its habit of nesting in caves, no subfossil remains have been found in the rich fossil deposits on the Plaine Corail, which suggests that

TABLE 3. List of endemic Mascarene bird species mentioned in the text, with percentages of scientifically described species and undescribed species known from the fossil record. This study has shown that certain families of birds are under-represented in the literature, especially the sea birds and passerines. The high number of undescribed taxa on Réunion is a result of the poor fossil record from that island (see also Table 2). Key: \dagger =extinct; *=species occurs on more than one island.

Family	Endemic species described/ undescribed	% of species undescribed	Mauritius	Réunion	Rodrigues
Anatidae	3/2	66%	2†*	2/1 **	1 🕆
Procellariidae	2/1	50%	_	2	1†
Threskiornithidae	1/0	0%	_	1†	-
Ardeidae	3/0	0%	1 🕇	1 †	1†
Sulidae	0/1	100%	1 👬	_	1 †*
Phalacrocoracidae	0/1	100%	1 🕆	1†	-
Falconidae	3/1	33%	1	1/1 †	-
Accipitridae	1/0	0%	1 **	1*	-
Rallidae	4/2	50%	2/1 **	2/1 **	1†
Columbidae	12/3	25%	5(4†)	1/3†	2/0†
Psittacidae	9/2	22%	3(2†)/0	4/2 †	2/0†
Strigidae	3/0	0%	1 🕇	1 †	1†
Campephagidae	2/0	0%	1	1	-
Monarchidae	1/0	0%	1*	1*	-
Pycnonotidae	2/1	50%	1	1	1†
Sylviidae	1/0	0%	_	_	1
Zosteropidae	4/0	0%	2	2	-
Sturnidae	2/1	50%	1 🕆	1†	1†
Muscicapidae	1/0	0%	_	1	_
Ploceidae	3/0	0%	1	1†	1

swiftlets were absent from Rodrigues.

Passerines

Passerines have been particularly successful at colonising remote oceanic archipelagos; however, establishing their former diversity can be problematic. Passerines were rarely mentioned in the early Mascarene literature and, where passerine fossil remains have been collected, there has been a tendency to ignore them. Here I present a preview of my recent findings; even in this initial period of study, a number of new taxa have been discovered (see also Tables 3 and 4).

Cuckoo shrikes (Campephagidae)

Cuckoo-shrikes are endemic to Mauritius and Réunion, but there is no evidence that *Coracina* ever occurred on Rodrigues.

Coracina typica — The Mauritius cuckoo shrike is widespread on the island, but it is declining in numbers and considered endangered (SINCLAIR & LANGRAND 2004). I identified subfossil remains from cave deposits collected by THIRIOUX around Le Pouce Mountain.

Coracina newtoni — The Réunion cuckoo shrike is critically endangered and restricted to two small plateaus, the Plaine d'Affouches and Plaine des Chicots, in the north-west (LE CORRE & SAFFORD 2001). No subfossil remains are known, which is unsurprising considering its montane habitat.

Monarch-flycatchers (Monarchidae)

Terpsiphone bourbonnensis — The Mascarene flycatcher is divided into two subspecies, *T. b. bourbonnensis* (STATIUS MÜLLER, 1776) on Réunion and *T. b. desolata* (SALOMONSEN, 1933) on Mauritius. Both populations remain comparatively scarce, but they have a widespread distribution where suitable habitat remains. Flycatchers have not been found in any Mascarene fossil deposit, and the genus is absent from Rodrigues.

Swallows (Hirundinidae):

Phedina borbonica borbonica — The Mascarene

swallow is found on Mauritius and Réunion and may have been vagrant to Rodrigues in the passed. It is not known from the fossil record, but it is unlikely that the present status is any different now than in pre-human times (CHEKE 1987).

Bulbuls (Pycnonotidae)

Hypsipetes olivaceus — The Mauritian bulbul or merle was considered a delicacy (STAUB 1976; CHEKE 1987), so it is one of the few passerines that can be identified from the early literature on Mauritius. It is considered endangered today. A number of subfossil remains were collected by THIRIOUX around the valleys of Le Pouce and caves at the Plaine des Roches.

Hypsipetes borbonicus — The Réunion bulbul was also regularly mentioned due to its edibility (*e.g.*, DUBOIS 1674). It is widespread on Réunion and considered of least concern, but numbers are declining. No subfossil remains have yet been discovered.

Hypsipetes sp. — CowLES (1987: p. 99) mentioned but did not describe a *Hypsipetes* bulbul collected in 1974 from caves on the Plaine Corail. I have since identified a number of cranial and post-cranial elements discovered in Caverne Poule Rouge, Caverne Bambara II and Caverne Gastonia. A Rodrigues bulbul was never recorded in the early literature, so the reasons for its extinction are unclear.

Old World warblers (Sylviidae)

Acrocephalus rodericanus — The Rodrigues warbler is endemic to Rodrigues, and although presently restricted in range, it once occurred all over the island (NEWTON 1865). Cranial and postcranial remains of this species have been collected from Caverne l'Affouche, Caverne Gastonia and Caverne Bambara on the Plaine Corail. There is no present evidence to suggest that Acrocephalus ever occurred on Mauritius or Réunion, but a related species occurs on the Seychelles.

White eyes (Zosteropidae)

The white-eyes are successful oceanic island colonists and inhabit numerous islands within the Western Indian Ocean (SINCLAIR & LANGRAND

2004); the Mascarenes were almost certainly colonised by *Zosterops* twice in their history (WARREN *et al.* 2006), but the genus has never been recorded on Rodrigues.

Zosterops chloronothos — The Mauritius olive white-eye is now rare on Mauritius, and confined to the Black River Gorges mountain range. I identified it from THIRIOUX' subfossil cave material collected around Le Pouce Mountain and Plaine des Roches in central Mauritius, which shows that it was once more widespread on the island.

Zosterops olivaceus — The Réunion olive white-eye is common and widespread, occurring in the highlands as well as the lowlands. No subfossil remains have yet been discovered.

Zosterops borbonicus — The Réunion grey white-eye is endemic to Réunion (SINCLAIR & LANGRAND 2004), where it is widely distributed. Despite this, no subfossil remains have yet been found.

Zosterops mauritianus — The Mauritius grey white-eye is sometimes considered to be a subspecies of *Z. borbonicus*. It is extremely adaptable and it is the commonest surviving native bird. I identified post-cranial subfossil remains from THIRIOUX' cave deposits collected around Le Pouce Mountain and Plaine des Roches.

Starlings (Sturnidae)

The starlings are gregarious, medium to largesized birds that inhabit forests and open woodlands (CRAIG & FEARE 2009). Each Mascarene island once harboured an endemic species, two of which were described in early accounts, but only the Réunion species has been preserved as skins. MtDNA analysis has shown that a unique skin, supposedly representing another species of Rodrigues starling *Necropsar leguati* FORBES, 1898, is actually an albinistic trembler from the West Indies (OLSON *et al.* 2005). My re-examination of a sternum of a supposed babbler (Timaliidae), mentioned but not described by COWLES (1987: p. 99), is referable to *Necropsar rodericanus*.

Fregilupus varius — The Réunion crested starling or huppe was reported as common until the late 1840s (CHEKE & HUME 2008). However, it appeared to have disappeared extremely rapidly, probably as a result of habitat destruction and over-hunting (HUME unpubl. data), with the final records being made in the 1850s (CHEKE & HUME 2008). The huppe is characterised by a distinct crest, long, decurved bill and robust pelvic elements. There may have been pronounced sexual dimorphism, the males being larger, with a longer, more decurved bill. MtDNA analysis has shown that *Fregilupus* is distantly related to southeast Asian Sturnus starlings (ZUCCON et al. 2008). At least 20 skins have been preserved in various museums, but a distal femur fragment found in the Grotte des Premiers Française is the only subfossil so far discovered on Réunion (MOURER-CHAUVIRÉ et al. 1999).

Mauritius Starling — I identified a number of cranial and post-cranial bones of a starling from THIRIOUX' material collected around Le Pouce Mountain and Plane des Roches. This new taxon differs markedly from the other Mascarene starling genera and warrants generic status (HUME in press). Most notable is the long, decurved bill with elongate, well-developed retroarticular processes. This suggests that it was a powerful gaper. The Mauritian starling was not mentioned in the literature, so the reasons for its disappearance are unknown.

Necropsar rodericanus — The Rodrigues starling is known from 19th century subfossil remains, and recently collected material from Caverne Poule Rouge, Caverne Bambara II,

TABLE 4. A total of 57 endemic Mascarene birds have been scientifically described, but another 21, all extinct and known only from the fossil record, await description. The passerines make up 28% of the total number of endemic birds, with at least another 6 undescribed, making them the least described Mascarene order of birds. Key: \dagger =extinct; E=extant; *=*Anas theodori*, *Circus maillardi* and *Fulica newtoni* occurred on both Mauritius and Réunion, but have been included here as part of the total of each island.

Totals	Described/ undescribed	Percent of unde- scribed species	Mauritius	Réunion	Rodrigues
Total number of Passerines/	16/6	37%	6E/4†	8(2†)/0	3(1†)/2
Total number of endemic birds	57/21	36%	28/8*	32/9*	13/6

HUME: A synopsis of the pre-human avifauna of the Mascarene Islands

Caverne Dora, Caverne Gastonia and Caverne Tortue on the Plaine Corail. It is also known from a unique account. In 1725–26, TAFFORET (HUME & WALTERS 2012) observed birds on the southern islets, where he described their ability to tear turtles (juvenile tortoises?) out of their shells. PINGRÉ in 1761 (NAGAPEN 2004) did not mention them, so it is likely that they had died out in the intervening years. The Rodrigues starling was slightly smaller than *Fregilupus*, with a straighter, more robust bill and more robust pelvic elements.

Stonechats (Muscicapidae)

Saxicola tectes — The Réunion Stonechat occurs only at higher elevations on Réunion, and is common along forest fringes and on heathland (SINCLAIR & LANGRAND 2004). Due to its montane habitat and the lack of high elevation fossil deposits, no subfossil remains of *S. tectes* have been discovered.

Weavers (Ploceidae)

The *Foudia* fodies are endemic to Indian Oceanic islands, including Madagascar, and the Mascarenes once harboured three endemic species, with Madagascan *Foudia madagascariensis* (LINNAEUS, 1766) also introduced to all three islands by humans. The Madagascan Fody was originally brought in as a cage bird, becoming established on Mauritius and Réunion in *c*. 1770, and sometime before 1916 on Rodrigues (CHEKE 1987; CHEKE & HUME 2008)

Foudia rubra — The Mauritius fody is now extremely rare and restricted in range, but is one of the few small passerines mentioned in the early literature (CHEKE 1987). I identified cranial and post-cranial subfossil remains from cave deposits collected around le Pouce and Plaine des Roches, indicating that it once had a wide range over Mauritius.

Foudia delloni — The Réunion fody was considered a serious pest when first known in the 1670s (DUBOIS 1674; DELLON 1685), but disappeared with extreme rapidity shortly after (HUME & WALTERS 2012). No subfossil remains are known.

Foudia flavicans — The Rodrigues fody had declined to less than 20 birds in the 1960s

and was confined to the central plateau (CHEKE & HUME 2008), but it is now increasing in numbers and naturally extending its range. I collected post-cranial and cranial subfossil remains from Caverne Gastonia and Caverne l'Affouche.

Passeriformes incertae sedis

Sharp-billed finch — Mauritius. Among the subfossil remains collected by THIRIOUX is a possibly associated premaxilla and rostrum mandibulae, which represent a new taxon. The bill is long and pointed, and intermediate in size between the undescribed Mauritius starling and *Hypsipetes*. Its generic affinities have not yet been determined.

Broad-billed finch — Mauritius. A fragmentary rostrum mandibulae and a series of post-cranial elements differ from all other Mauritian passerines. They appear to belong to a small species with a broad bill, similar to but larger than *Foudia rubra*, a species found in the same deposits.

Long-legged finch — Mauritius. A distinct tarsometatarsus, much longer and more gracile than any other Mascarene passerine, almost certainly belongs to a new taxon. The osteology suggests that it was a terrestrial species, but its relationships are at present unclear.

Intermediate finch. Rodrigues. A series of post-cranial elements belong to a passerine intermediate in size between the undescribed *Hypsipetes* bulbul and *Foudia flavicans*. Its affinities cannot yet be determined, but it almost certainly represents another now-extinct taxon from Rodrigues.

Discussion

Biogeography

The importance of sea level fluctuations and prevailing wind and sea currents in facilitating avian dispersal and colonisation events within the southwestern Indian Ocean is now being recognised. Indian subcontinental winter Monsoon winds, along with winds from the direction of Australia and Indonesia blow across the Indian Ocean towards the Madagascar region, a route also followed by ocean currents (CHEKE & HUME

2008; WARREN et al. 2010). Numerous sea level low stands of up to 50 m lower than present have been recorded in the last 5 Ma (MILLER et al. 2005), whereas in the last 650 Ka, some sea level low stands were up to 135 m lower than present, and persisted for up 50 Ka at a time (WARREN et al. 2010). These events would have greatly increased the land-surface area of the Maldives, Seychelles and Mascarenes, and created subaerial island archipelagos in the Chagos, the Saya de Malha, Nazareth and St.Brandon (Cargados Carajos) banks. This not only reduced distances between islands and continental land masses, but also the inter-island crossings; thus the avifauna could encompass vast stretches of ocean via island-hopping. This may explain why much of the Mascarene avifauna has its origins in Southeast Asia (WARREN et al. 2010), and not in Madagascar or Africa (AGNARSSON & KUNT-NER 2012), the nearest large landfalls. Although the origins of some Mascarene genera remain unresolved, mtDNA studies have shown that Psittacula (GROOMBRIDGE et al. 2004); Alectroenas (GIBBS & PENNY 2010; PEREIRA et al. 2007; SHAPIRO et al. 2002); Raphus and Pezophaps (PEREIRA et al. 2007; SHAPIRO et al. 2002); the Mascarene Zosterops (WARREN et al. 2006); Hypsipetes (WARREN et al. 2005) and Fregilupus (ZUCCON et al. 2008) all had their origins in Southeast Asia. Interestingly, the Madagascar endemic starling genus Hartlaubia is the closest to the Mascarenes biogeographically, but differs completely in morphology from the Mascarene sturnids. Furthermore, the Seychelles scops owl Otus insularis (TRISTRAM, 1880) is more closely related to Southeast Asian Otus than to those occurring in Africa (FUCHS et al. 2008).

While the origins of some genera remain unresolved, *e.g.*, *Aphanapteryx*, *Eurythromachus*, the founding populations of *Nesoenas*, *Alopochen*, *Threskiornis* and *Saxicola* almost certainly lie within Madagascar, whereas others, *e.g.*, *Foudia*, are Indian Ocean island endemics. *Threskiornis* and *Saxicola* are unknown on Mauritius and Rodrigues, which may have been due to the lack of suitable montane heathland habitat in the case of *Saxicola*, or competitive exclusion. Mauritius and Rodrigues already had a diverse range of terrestrial birds, especially rails, which may have prevented *Threskiornis* from becoming established. Furthermore, Réunion lacks the genera *Raphus*, *Pezophaps*, *Lophopsittacus* or *Necropsittacus* parrots, and *Aphanapteryx* or *Erythromachus* rails. MOURER-CHAUVIRÉ *et al.* (1999) postulate that these genera may have once occurred on Réunion, but disappeared due to the Piton des Nieges volcanism that occurred between 300 to 188 Ka. Thus the avifauna of Réunion is of comparatively recent origin. Apart from the probably poorly volant or flightless Réunion rail *Dryolimnas augusti*, this may explain why none of the Réunion avifauna that survived into the historic period had evolved complete flightlessness, a characteristic so prevalent with birds on Mauritius and Rodrigues.

There are a number of other perplexing paradoxes. The passerine genera Zosterops, Coracina and Tersiphone appear to have colonised Mauritius and Réunion only, whereas Acrocephalus seems to be restricted to Rodrigues. There are also other southwestern Indian Ocean passerine genera, e.g., Copsychus, Nectarinia, which occur in the Seychelles and Madagascar that are not present on the Mascarenes. Is this a natural distribution, or is there a bias in the fossil record? The Hypsipetes bulbuls that occur in the Mascarenes occur only on Mauritius and Réunion today, but the discovery of a fossil Hypsipetes species on Rodrigues has shown that each island once had its own species. Likewise, starlings were thought to be restricted to Réunion and Rodrigues, but my recent discovery of a fossil sturnid has revealed that an endemic species also once occurred on Mauritius. Therefore, as the islands have suffered severe anthropogenic changes and the fossil record is far from complete (see Tables 3 and 4), any conclusions based on present avian biogeography must be viewed with caution.

Comparison of the island avifaunas

Documentation left by early vistors to the Mascarene Islands and the fossil record have provided a robust insight into the former avian diversity of the islands. However, this is based in part on how fully the palaeontological record represents the avifauna that was in existence at the time of deposition. Each Mascarene island differs topographically, and although the islands may have shared some genera, the processes of evolution unique to each island resulted in differing speciation events. It appears that once established, much of the Mascarene avifauna became sedentary, with little mobility between islands; the notable exceptions being Fulica, Anas, Psittacula and perhaps Nesoenas turtle doves that appeared to have migrated between Mauritius and Réunion (CHEKE & HUME 2008; MOURER-CHAUVIRÉ et al. 1999). All of the species mentioned in accounts on Mauritius and Rodrigues have now been correlated to some degree with subfossil remains, whereas the recently discovered and undescribed fossil taxa discussed above were never recorded in life. This is certainly not the case with Réunion. The paucity of fossil remains on Réunion has compounded research problems, and left the affinities of a number of taxa unresolved (see Tables 2, 3 & 4). Cecilé MOURER-CHAUVIRÉ and her co-workers have done much to rectify this shortfall, yet Réunion remains the poorest island palaeontologically. That a cormorant, a Porphyrio rail, three parrots, a pigeon and a fody once occurred on Réunion is beyond doubt, yet they lack physical evidence of any kind. Even extant species such as the Réunion harrier, which is known from the fossil record on Mauritius and all extant passerines, are unknown in the Réunion palaeontological record. This may be the result of a fossil depositional bias, as Réunion has few caves, and only one fossiliferous swamp. MOURER-CHAUVIRÉ et al. (1999) have shown that the Marais de l'Ermitage was subject to hydrological sorting; hence the lack of small bird elements.

Centuries of occupation

The Mascarenes have been subject to severe anthropogenic changes for over four centuries, which unsurprisingly has led to high extinction rates. Human impact on the Mascarenes occurred in approximately five phases:

1. Arab period 1300–1500 — Records of Arab traders on the Mascarenes do not exist, but by inference it can be determined that they were aware of the islands from at least the 13th century (NORTH-COOMBES 1994a), or 14th century. As far as known, no attempt at settlement was made, but 14C dates obtained from a black rat *Rattus* aff. *rattus* mandible collected from the Mare aux

Songes, and from a rat-predated extinct terrestrial snail, Tropidophora carinata, both provide dates of 590±27 BP (interval in real years after calibration 1369–1413 AD) (HUME Unpbl. data). Arab traders had thus inadvertently introduced black rats nearly 200 years before the arrival of the Dutch. Mainland Mauritius once harboured a diverse range of endemic snakes and terrestrial reptiles, including the world's largest skink, but these were never mentioned in the historical literature. Early accounts from Mauritius are notorious for the lack of descriptive information about the smaller birds and reptiles (CHEKE & HUME 2008), so there is a strong possibility that they were simply not mentioned, especially if they were inedible or not worthy of eating. However, it is extremely likely and as the fossil record has shown (see passerines above), that components of the herpetological fauna and some passerines disappeared as a direct result of the early introduction of black rats.

2. Portuguese period 1510–1528 — The Portuguese first encountered Réunion in 1510, Mauritius in 1516, and Rodrigues in 1528 (NORTH-COOMBES 1994a), but appear to have landed only rarely. The Portuguese fleets were under strict state order not to disclose trading details (MOREE 1998), so very few records were made. North-Coombes recorded one landing on Réunion by a Portuguese ship in 1528, after which livestock (probably goats) were released to provide fresh meat on future visits.

3. Dutch period 1598–1710 — The Dutch claimed Mauritius for the Netherlands in 1598 and maintained an almost continuous colony until 1710 (MOREE 1998). The busiest shipping period took place from 1601 until 1612, after which the island was only sporadically visited. A fort was built in 1638, but the Dutch abandoned Mauritius in 1658, before re-establishing a colony in 1664. By 1710 the island was no longer considered to be worth maintaining, and was completely abandoned. The European population on Mauritius never numbered more than 50 at any one time, but escaped slaves settled in the interior (HUME 2006). Deforestation was confined to coastal and lowland regions, but the Dutch introduced many non-native species. It was during this period that all large and flightless birds, including the dodo, disappeared.

Two Dutch fleets visited Réunion and left reports, the first led by Adriaen BLOK in 1612, and another led by Willem BONTEKOE in 1619 (CHEKE & HUME 2008), but the Dutch never settled on the island. BONTEKOE in particular remarked on the abundance and inherent tameness of the fauna.

A fleet under Admiral Wolphert HARMENS-ZOON sailing in the flagship, *Gelderland*, landed on Rodrigues in 1601 and recorded brief details about the island and its fauna (MOREE 2001; HUME 2003), but it was not until the arrival of Francois LEGUAT in 1691 that detailed faunal descriptions were made (LEGUAT 1708). Rodrigues was still in a comparatively pristine state during this time, but LEGUAT noted the presence of large numbers of rats. After two years stay, LEGUAT left Rodrigues for Mauritius and and made a brief faunal report, in which he mentions that rails, ducks, geese and pigeons had become rare.

4. French period 1642-to present (Réunion); 1715-1810 (Mauritius); 1736-1809 (Rodrigiues) — The French claimed Réunion (Bourbon as it was called from 1649) for France in 1642, and a permanent French colony was established in 1665, numbering up to 200 by 1674 (CHEKE & HUME 2008). DUBOIS (1674) in particular gave a good account of the fauna during the early years of occupation. Réunion remained comparatively pristine at this time, and DUBOIS in 1671-72 noted the absence of rats. However, this situation was to change drastically. By 1676, rats had reached plague proportions (CHEKE & HUME 2008), and combined with over-hunting, by the 1730s all of the endemic non-passerines were extinct. The British took control of the island in 1810, but it was restored to France in 1815 (LEGUEN 1993). In the following decades, a combination of increasing population, especially after the emancipation of the slave population in 1848, deforestation and over-hunting resulted in the extinction of Fregilupus varius (HUME & WALTERS 2012).

In 1715, the French claimed Mauritius for France, renaming it 'Isle de France', and established a permanent colony. Over the next 85 years, hunting and large scale deforestation took place. This resulted in the extinction of almost all of the remaining non-passerines, including the endemic pigeons, *Nesoenas cicur* and *Columba thiriouxi*, and parrot, *Psittacula bensoni* (HUME 2007, 2011).

On Rodrigues in 1725-26, a Réunionese mariner, Julien TAFFORET, was sent to report on its suitability for French occupation (NORTH-COOMBES 1971). He left a detailed account about the fauna and flora; little had changed since the time of Leguat, but he noted that birds were avoiding the mainland, which was almost certainly due to the presence of rats. TAFFORET reported the abundance of giant tortoises Cylin*draspis* sp., which resulted in the establishment of a tortoise-collecting station (North-Coombes 1994b). Although deforestation was negligible at this time, the introduction of cats around 1745 proved catastrophic. Just 16 years later, during the visit in 1761 of Guy Abbé PINGRÉ, who was on Rodrigues to measure the Transit of Venus (NAGAPEN 2004), a number of bird extinctions had taken place. PINGRÉ noted that the night herons, pigeons, owls, starlings and probably the solitaire had vanished, and that both species of parrot were extremely scarce, Necropsittacus rodericanus particularly so. When Philibert MARRAGON settled on Rodrigues in the 1790s and wrote an account of the fauna (North-Coombes 1971), only the Rodrigues parakeet Psittacula exsul and two passerines survived.

5. British period 1810–1968 — The British forcibly took Mauritius and Réunion in 1810 after establishing a military presence on Rodrigues, but returned Réunion to France in 1815 (TOUSSAINT 1972; NORTH-COOMBES 1971; LEGUEN 1993). On Mauritius, deforestation accelerated to make way for sugar cane production, and the remaining areas of mountain forest were exploited (CHEKE & HUME 2008). The last Mauritius blue pigeon was taken in 1837 (HUME 2011), and the last Mauritian lizard-owl around the same time, but three non-passerines, the pink pigeon *Nesoenas mayeri*, echo parakeet *Psittacula echo*, and Mauritius kestrel *Falco punctatus* survived in mountain forest in the Black River Gorges.

On Rodrigues, slash and burn agricultural practices and high populations of free-range livestock for export to Mauritius combined to destroy or fragment the last remaining forests. In 1874, a second Transit of Venus expedition organised by the Royal Society arrived on Rodrigues, which included the botanist Isaac BALFOUR. BALFOUR (1879: p.302) recorded that 'The great and tall trees have now almost entirely disappeared, the eternally verdant canopy formed by their boughs no longer exists, and the "little Eden" is now a dry and comparatively barren spot, clothed with a vegetation mainly of social weeds, and destitute of any forest growth save in unfrequented and more inaccessible parts in the recesses of the valleys'. This was also the last time that the Rodrigues parakeet, the only surviving endemic, non-passerine bird, was observed.

This study has shown that the avifauna of the Mascarenes has been subject to extremely high extinction rates over a comparatively small period of time. The wealth of documentation that exists has provided some indication as to why and when these events took place. Without exception, the extinction of all bird species was due to human activity. Direct hunting was more prevalent on Réunion than Mauritius and Rodrigues, whereas habitat destruction, particularly in the lowlands, seriously impacted on all three islands. However, it was the introduction of exotic animals that appears to the primary cause. The principal introductions included: black rats (c. 1400 on Mauritius, c. 1676 on Réunion, c. 1675 on Rodrigues); goats (c. 1606 on Mauritius, probably earlier (1528?) on Réunion, c. 1730 on Rodrigues); monkeys (c. 1606 on Mauritius); pigs (c. 1606 on Mauritius, c. 1620s on Réunion, c. 1790 on Rodrigues); cattle (c. 1606 on Mauritius, c. 1645 on Réunion, c. 1840 on Rodrigues); deer (c. 1638 on Mauritius, c. 1760 on Réunion, 1860 on Rodrigues); cats (c. 1688 on Mauritius/ Réunion, c. 1745 on Rodrigues); and brown rats Rattus norvegicus (c. 1730 on Mauritius/Réunion, c. 1870 on Rodrigues) (see CHEKE & HUME 2008 for a comprehensive list). Of all the introductions to the Mascarenes, the black rat was by far the worst invasive. This ferocious predator was directly responsible for the extinction or reduction in ranges of the majority of smaller birds, predated the eggs and chicks of the larger terrestrial birds, and competed with all native avifauna for limited food resources.

The fossil record has provided evidence of higher rates of extinction than previously realised, and more species await description. Therefore, caution should be applied when interpreting biogeography within the region. This is particularly pertinent to the fossil record of the smaller avifauna, especially passerines, on which little work has been undertaken, and those species inhabiting the more vulnerable lowland areas.

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